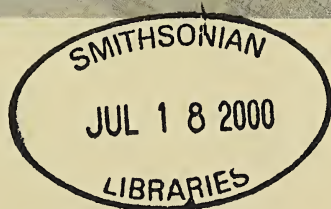


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Cover photo: An ant mimic (Family Clubionidae: *Myrmecium* sp.) from Trinidad. (Photo by Joe Warfel of Arlington, Massachusetts)

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THE FAMILY GALLIENIELLIDAE (ARANEAE, GNAPHOSOIDEA) IN THE AMERICAS

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ABSTRACT. *Azilia leucostigma* Mello-Leitão 1941 considered by Mello-Leitão as a metine (Tetragnathidae), is transferred to the gnaphosoid family Gallieniellidae, as the type species of the new genus *Galianoella*. The obliquely depressed endites, the flattened irregular posterior median eyes, and the conical anterior lateral spinnerets retaining a sclerotized distal ring, among other characters, clearly place the new genus in the family Gallieniellidae. *Galianoella leucostigma* is the only gallieniellid so far recorded from the Americas. This species has a specialized ant-preying behavior. Ant-preying may prove to be characteristic for all the family, as it was suspected in the Madagascan *Gallieniella*; and it may be associated with the modified chelicerae typical of the family.

Keywords: Spiders, arachnids, *Galianoella*

The family Gallieniellidae is a small family of dionychan spiders recorded so far only for Madagascar, the Comoro Islands, southern Africa, and Australia. Only a handful of papers have dealt with the group. Platnick (1984) summarized its taxonomic history and revised the family, describing several new species and the genus *Legendrena*; Platnick (1990b) added some species in *Gallieniella* Millot 1947 and *Legendrena*; Platnick (1990a) transferred *Drassodella* Hewitt 1916 from the Gnaphosidae and mentioned the existence of undescribed genera of Australian gallieniellids.

The gallieniellids have the obliquely depressed endites and flattened irregular posterior median eyes typical of the Gnaphosoidea, but they are probably the sister group of most other gnaphosoids because they have the anterior lateral spinnerets conical and more closely set than in most other gnaphosoid families and retain an apical segment (Platnick 1984, 1990a). These spiders are quite uncommon in collections, and very little is known of their biology. During recent years, several specimens of Gallieniellidae have been collected in dry and semi-arid habitats of northwestern Argentina. These were first thought to represent an undescribed genus and species. The species, however, had been described (as a metine tetragnathid!) by Mello-Leitão (1941), with the name *Azilia leucostigma*, which is here designed as the type species of the new genus *Galianoella*. Although Mello-

Leitão gave measurements for both the male and the female of *A. leucostigma*, the female was not illustrated, and the only specimen now available seems to be the male holotype.

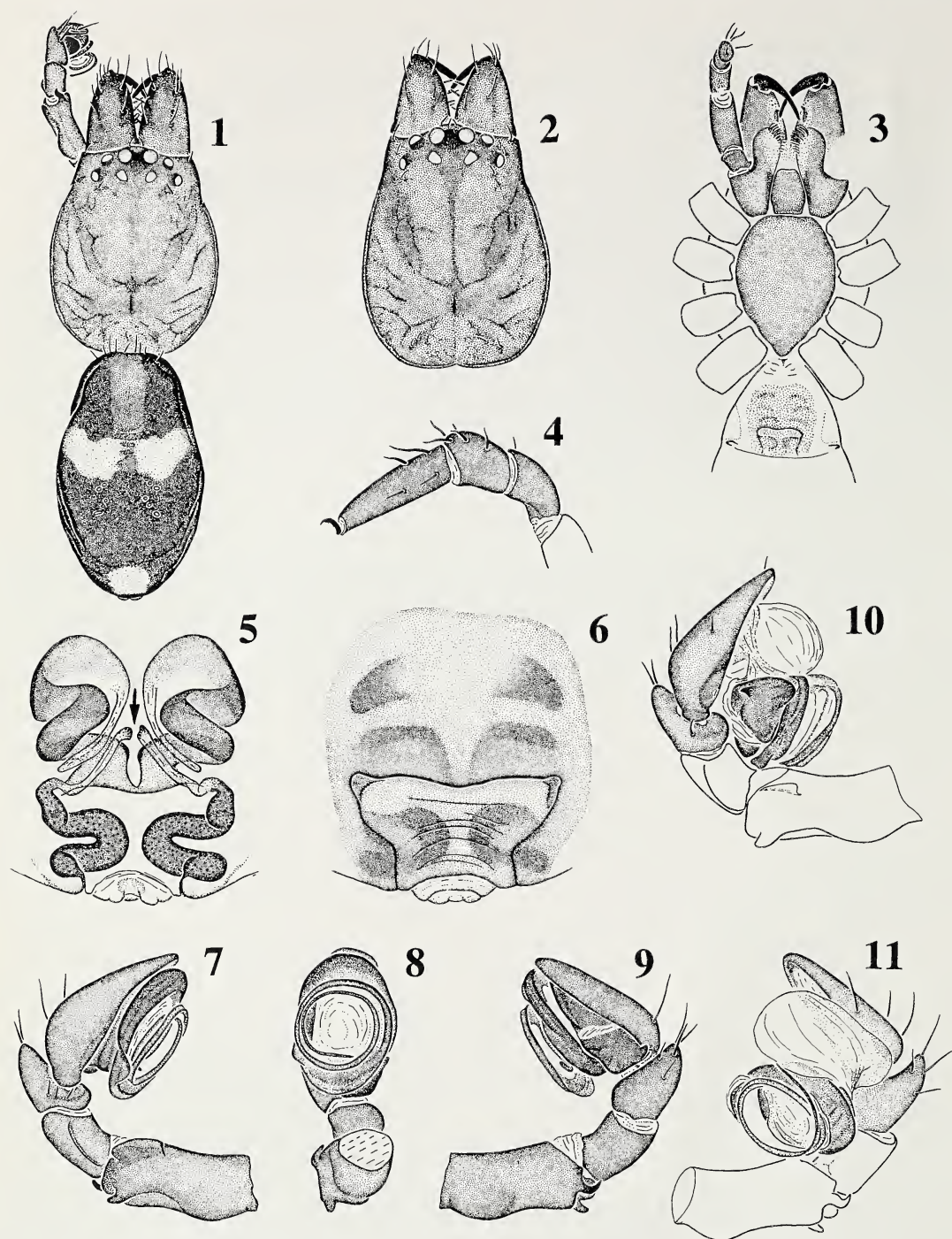
The abbreviations used in this study are standard for the Araneae. The notation for leg spines is as in Goloboff (1995). The specimens examined are deposited in the Instituto and Fundación Miguel Lillo, Tucumán, (FIML); Museo Argentino de Ciencias Naturales, Buenos Aires, (MACN); Museo de Ciencias Naturales, La Plata (MLP); and American Museum of Natural History, New York (AMNH).

Galianoella new genus

Type species.—*Azilia leucostigma* Mello-Leitão 1941.

Etymology.—It is a pleasure to name the new genus after María E. Galiano, who introduced me to arachnology, with gratitude for her continued help and advice, and in recognition of her contributions to arachnology.

Diagnosis.—*Galianoella* can be distinguished easily from other gallieniellid genera by the membranose area on the cheliceral margins (Fig. 3), and the eyes occupying a wider portion of the head (Figs. 1, 2). Females can be distinguished also by the laterally depressed palpal tibia with strong prolateral spines (Fig. 4) and the wrinkled membranous posterior extensions of the epigynum (Fig. 6). Males can be recognized by the complex pal-



Figures 1-11.—*Galianoella leucostigma*. 1, Dorsal view, male; 2, Dorsal view, female; 3, Ventral view, female; 4, Right female palp, prolateral; 5, Spermathecae; 6, Epigynum; 7-9, Right male palp, bulb in resting position; 10, 11, Right male palp, bulb expanded.



Figures 12–14.—*Galianoella leucostigma*. 12, Female with egg-sac; 13, Cell; 14, Detail of cell entrance.

pal femoral apophyses and keel (Figs. 7–9; absent in other genera of the family) and by the spiralled tegulum coiling around an extensive distal haematodocha (Figs. 8, 11).

Description.—See species description.

Relationships.—Their reduced number of cylindrical gland spigots suggests that *Legendrena* and *Gallieniella* are sister groups; in different gnaphosoid families, as well as in *Galianoella* and *Drassodella*, those spigots are usually fairly numerous (and often arranged in longitudinal rows; see Platnick 1990a). The eyes are set on a low tubercle in *Gallieniella*, *Legendrena*, and *Drassodella*, but are completely sessile and occupy most of the cephalic width in *Galianoella* and non-gallieniellid gnaphosoids, suggesting that *Galianoella* is the sister group of the other three genera.

The hypothesis of relationships just proposed, however, is far from well supported, as it is contradicted by the elongated and inclined chelicerae of *Gallieniella* and *Galianoella*. *Drassodella* and *Legendrena* have shorter, more vertical chelicerae, which suggests that *Galianoella* and *Gallieniella* are sister genera.

Besides the wider eye group, there are several other characters in which *Galianoella* differs from all other gallieniellids, but they are most parsimoniously interpreted as its autapomorphies. These autapomorphies include the membranose cheliceral areas, the interior cheliceral faces with short spiniform setae, the undifferentiated cheliceral margins, the ventral spines on patellae, the wrinkled posterior epigynal extensions with a cavity, the ring-like tegulum with an extensive haematodocha, the modified female palpal tibia bearing strong prolateral setae, and the modified male palpal femur. Although its absence in the other

gallieniellid genera cannot be ascertained from published illustrations of male palps, the subtegular projection is absent in *Gallieniella* (the only genus for which I have examined males). Thus, this projection may be another autapomorphy of *Galianoella*.

Galianoella leucostigma (Mello-Leitão 1941)
new combination

Figs. 1–14

Azilia leucostigma Mello-Leitão, 1941: 155, fig. 50, pl. 7, fig. 33 (male holotype, from Argentina, Province of Salta, Salta, M. Birabén col., no date, MLP 14808, examined).

Diagnosis.—See diagnosis for genus.

Description.—*Female*: (From Chuscha). Total length 5.91 (6.78 with chelicerae). Cephalothorax (Fig. 2) 2.34 long, 1.83 wide. Cephalic region almost flat, 1.62 long, 1.38 wide. Eyes occupying 0.78 of head width, in two recurved rows; AME rounded, convex, on low common elevation; all other eyes completely sessile; PME irregular, flattened, with diffuse limits. Chelicerae elongated (Fig. 3), with long fang, with about 60 small spiniform setae on interior face, larger and stronger near anterior face. Chelicerae distally narrow, with pro- and retromargins not well differentiated; with membranose area apically wider (visible only from below); single, large (retromarginal?) tooth and 2 small denticles set on common sclerotized elongate patch in the middle of this membranose area, 2 or 3 small (promarginal?) denticles on apex. Endites long, medially constricted; labium 0.56 long, 0.42 wide, flat; sternum 2.60 long, 1.20 wide. Intercoxal bridges not visible. Palpi (Fig. 4) short; tibia short, laterally compressed, with strong prolateral erect setae. Legs long, slen-

Table 1.—Leg measurements (in mm) of *Galianoella leucostigma*.

Female	Femur	Patella + Tibia	Metatarsus	Tarsus	Total
I	2.16	2.76	2.07	1.20	8.19
II	1.98	2.46	1.98	1.11	7.53
III	1.83	2.28	1.80	0.84	6.75
IV	2.28	2.91	2.43	1.08	8.70
Palp	0.72	0.72	—	0.66	2.10
Male	Femur	Patella + Tibia	Metatarsus	Tarsus	Total
I	2.12	2.76	2.12	1.24	8.24
II	2.00	2.28	2.00	1.08	7.36
III	1.88	2.24	1.80	0.88	6.80
IV	2.40	2.92	2.44	1.04	8.80
Palp	0.76	0.72	—	0.76	2.24

der; tarsi ascopulate, without claw-tufts; with few, weak spines. Measurements: See Table 1.

Chaetotaxy: Femora: I, 1 D (1:3 AP), 1 P SUP (1:4 AP); II-IV, 1-1-0 D; palp, 1 p (1:4 ap). Patellae: I, II, 1 d ap (thin, erect, on the condyle joining patella and tibia), 1 v post b; III, IV, 1 d ap (as in I, II), 0 v; palp, 1 d ap (weaker than in I, II). Tibiae: I, II, 0; III, 1 d (1:4 ap), 1 V ANT (1:5 B), 2 V AP; IV, 1 d (1:4 ap), 1-1-1 V ANT, 1 V POST AP; palp, 3 P SUP A (erect, curved), 3 P (shorter). Metatarsi: I, II, 0; III, IV, 1 V ANT (1:3 B). Tarsi: I-IV, 0; palp, numerous erect thin setae on V and P, 1-1 D ANT B, 1-1 P (1:3 B).

Palpal tibia laterally compressed (i.e., wider dorso-ventrally). Superior tarsal claws with single row of 3 teeth (basal one of III and IV bifid); third claw absent from all tarsi; palpal claw with 3 teeth, increasing in size from basal to distal. ALS conical, with distal sclerotized ring, with 2 spigots (with short, rather wide shaft distinctly separated from base; possibly corresponding to piriform glands, not SEM examined); PMS with larger spigot on apex (with base larger than shaft), plus 7 slightly smaller ones (possibly cylindrical, as they are absent in the male) on the dorsal face, in two alternate rows; PLS with 2 closely-set spigots on anterior edge, plus one medial spigot.

Coloration: Cephalothorax and legs reddish-brown; abdomen dorsally black, with two dorsal and single posterior yellow-cream areas; venter pale, darker laterally and around spinnerets. Epigynum: (Fig. 6). Large sclerotized plate, with posterior membranous wrinkles, with posterior opening connecting to in-

ternal cavity (apparently glandular). Spermathecae (Fig. 5) reniform; portion of copulatory ducts distal to spermathecae strongly sclerotized, spiralled; proximal portion twisted around most distal one, with medial glandular area (Fig. 5, arrow near strongly sclerotized edges of distal portion).

Male: (Chuscha). As in female, except as noted: Total length 5.31 (5.91 with chelicerae). Cephalothorax (Fig. 1) 2.40 long, 1.83 wide. Cephalic region 1.56 long, 1.32 wide. Eyes occupying 0.77 of head width. Labium 0.56 long, 0.42 wide; sternum 2.43 long, 1.20 wide. Leg measurements: see Table 1. Chaetotaxy: As in female, except: Tibiae III, IV, 1-1-2/1-0-1 V ANT, 1 V POST AP, 1 d (1:4 ap); palpal tibia with 5 setae on apex; cymbium with some thickened spiniform dorsal setae. Abdomen (Fig. 1) with dorsal anterior scutum. Spinnerets as in female; ALS spigots as in female; PMS and PLS with single large apical spigot. Palp (Figs. 7-11): Three dorsal apical apophyses on femur: anterior one pointed and strongly sclerotized, posterior one blunt, middle one rounded; retroventral apical keel on femur; retrolateral longitudinal keel on patella; tibia with dorsal long projection bearing strong setae. Bulb: Subtegulum very large, visible in prolateral view (Fig. 9), with small projection (Fig. 10) anchoring in the anterior basal rim of the cymbium; tegulum spiralled, almost continuous with strip-like spiralled embolus, coiling around large distal haematodocha occupying central position (Figs. 8, 11).

Natural history.—*Galianoella* lives under stones or logs, in arid or semi-arid habitats. The specimens were found in small silk cells

up to 2 cm long, 1 cm wide, sometimes covered with debris and prey remains, with two entrances. The entrances had a peculiar structure, with two small parallel flaps, each about 4 mm wide and with 15 small finger-like bars (formed by either a single thick thread, or several thinner threads compacted or cemented by some substance). These bars are about 1.5 mm long (half of which is imbedded in the silk mat), roughly parallel, and give the cell entrance the appearance of a double comb. Perhaps these peculiar combs help prevent ants from entering the refuge. The egg-sac is flattened, lenticular, 8–9 mm in diameter, with an internal white papery layer (as in many other gnaphosoids) and an outer layer of loose much thicker threads. Several cells contained more than a single egg-sac.

The living specimens, although not definitely myrmecomorph, have a strong ant-like appearance. They do not use their first legs as antennae (as many ant-mimicks do), but walk in a somewhat ant-like way; the resemblance to an ant is strengthened by the paler dots on the abdomen, which give the impression of a constriction. Especially because of the way they move, the first impression on seeing specimens in the field is of cell-living castaneirine corinnids with unusually long chelicerae and unusually bright PME (castaneirines do not live in cells, and have short vertical chelicerae and normal PME).

In captivity, the specimens were observed to feed only on ants. A few other items of prey were offered, but ignored. The cells of *Galianoella* often contained *Camponotus* remains (Formicidae, Formicinae), and it is likely that adults prey upon them; in captivity, the spiders were fed *Acromyrmex* (a leaf-cutting ant, Myrmicinae) and soldiers of *Pheidole* (the European fire ant, also a myrmicine). The Madagascan *Galieniella* have been collected together with ants, and it was suspected that they could prey upon them, but no actual observations exist.

The capture sequence in *Galianoella* is very stereotyped. The spider always attacks the ant from behind, placing its fangs on the sides of the ant's thorax. When the ant was not facing away from the spider (the most common situation), the spider positioned herself, moving around the ant sideways (i.e., always facing the ant), in an arc about 1 cm in diameter; when the ant continued crawling

(which happened most of the times), the spider followed the ant in the same manner for a few centimeters until she could position herself in a proper position to attack. While pursuing the ant, the spider walked on six legs, with her chelicerae wide open, the palpi raised and retracted, and the extended anterior legs raised at an angle of about 45°.

It is possible that the large tooth set on the sclerotized plate on the membranous cheliceral patch and/or the spine-like setae on the inner chelicerae (together with the palpi, see below) play a special role in holding the ant after the attack. It is also possible that the spider fangs were not actually piercing the ant's exoskeleton at this time (a couple catches were observed under the microscope, under low magnification); rather, the fangs seemed to embrace the ant's thorax and coxae, holding the thorax pressed against the basal article of the chelicerae. Sometimes the spider held the ant in this way for only an instant, quickly releasing and following it until it died (always within a few seconds). Often, the spider did not release the ant at all; while holding the ant, the spider palpi were put downwards (with apical articles directed posteriorly), such that the tibial spines when pressed against the ant's abdomen, and the ant's abdomen could then only curve downwards. The spider palpi were then not visible from above. Careful examination of the ant remains under light magnification (about 50×) revealed no holes, suggesting that the ant may be immobilized by a substance other than cheliceral venom. Jocque & Dippenaar-Schoeman (1992) have reported zodariid spiders subduing termites without biting them. Additional research is needed to determine whether that is the case in *Galianoella*, but it is not entirely unlikely that the unsclerotized cheliceral patches contain special glands that help in prey capture.

The laroniine *Eilica* Keyserling 1891, another ant-catching gnaphosoid spider sympatric with *Galianoella* (collected at El Hongo and Chuscha), also has peculiar cheliceral modifications. The specimens of *Eilica* that were actually observed catching ants were mixed with other specimens of *Eilica* from the same localities, but later study revealed that two species (*E. trilineata* Mello-Leitão 1941 and *E. modesta* (Keyserling 1891)) coexist there; and one of the spiders was found eating a worker of *Acromyrmex striatulus*. The ant-

catching behavior of *Eilica* (so far unknown), however, is quite different from the cautious behavior of *Galianoella*: the spider quickly ran onto the ant's head, bit the base of an antenna, quickly released the ant, and waited by the side for the ant to die (or at least, to become motionless; this occurred within a few seconds). The Laroniinae are characterized by a laminar (almost membranous) keel in the cheliceral margin. *Callilepis* Westring 1874, the other genus in the subfamily, has been reported to capture ants in a similar way (Heller 1976); and it is most likely that the cheliceral keel, synapomorphic for the subfamily, plays a special role here.

Distribution.—Southern Salta and northwestern Tucumán, in northwestern Argentina. The six known localities are all in two valleys which form part of a larger system of valleys, rather isolated from lower, more forested habitats. Relatively careful collecting in other parts of Salta and Tucumán has yielded no specimens of *Galianoella*, which may be restricted to these valleys.

Other specimens examined.—**ARGENTINA:** *Salta*: Chuscha, 6 km NW Cafayate, 10 January 1995 (P. Goloboff, C. Szumik), 2 ♀ (FIML); 18 April 1995 (P. Goloboff, C. Szumik), 2 ♀ (FIML); 20 November 1995 (P. Goloboff), 2 ♂ (FIML), 1 ♂ (MACN), 1 ♀ (AMNH). El Hongo, 2 km S Alemania, July 1995 (M. Ramírez, P. Goloboff) 1 ♀ (MACN). La Salamanca, 3 km S Alemania, 19 February 1996 (P. Goloboff, C. Szumik), 2 ♂ (FIML). Ruta Nacional 40, km. 1026, 6 km S Tolombón, 18 April 1995 (P. Goloboff, C. Szumik), 1 ♀ 3 juvs. (FIML). *Tucumán*: Amaicha del Valle, 10 January 1995 (P. Goloboff, C. Szumik), 1 juv. (FIML).

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I am grateful to Norman Platnick for the loan of comparative specimens of *Gallieniella*

la, *Legendrena*, and *Drassodella*; to C. Sutton, A. Brescovit, and A. Bonaldo for making the type specimen of *Azilia leucostigma* available; to Norman Platnick and Martín Ramírez for their critical comments on the manuscript; to the Consejo Nacional de Investigaciones Científicas y Técnicas for supporting my research; and to F. Cuezco for identifying ant remains.

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DESCRIPTIONS AND NOTES ON THE GENUS *PARADOSSENUS* IN THE NEOTROPICAL REGION (ARANEAE, TRECHALEIDAE)

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ABSTRACT. Three Brazilian species of the genus *Paradosenus* F.O. Pickard-Cambridge 1903 are included in this paper: *Paradosenus minimus* (Mello-Leitão 1940), whose holotype was located and is here redescribed; *Paradosenus corumba* new species is described from Mato Grosso do Sul, Brazil and preliminary data on its biology are presented. Morphological data and new records of *P. longipes* (Taczanowski 1874) are included.

Keywords: *Paradosenus*, Trachaleidae, Araneae, Neotropical region

The genus *Paradosenus* F.O. Pickard-Cambridge 1903 was revised by Sierwald (1993) and includes three neotropical species: *P. longipes* (Taczanowski), *P. pulcher* Sierwald 1993 and *P. caricoi* Sierwald 1993. In the same paper, she synonymized the monotypic genus *Xingusiella* (type species *X. minima*), described by Mello-Leitão (1940) based on the illustration of the epigynum and characters presented in Mello-Leitão's description. The author also suggested that "*P. minimus* might be a fourth valid species in the genus *Paradosenus*" (Sierwald 1993).

Recently the holotype of *Xingusiella minima* was found in the MNRJ collection, mixed with other material of the family Pisauridae. The examination of this specimen confirms Sierwald's supposition that the specimen belongs to this genus, and the species is here redescribed. While examining other Brazilian collections more *P. longipes* material was found, and its geographical distribution is here extended to include southern Brazil and northern Argentina specimens. A new species, *P. corumba*, much smaller than *P. minimus*, was collected by the second author (JR) in the project "Biodiversidade da Fauna Associada a Macrófitas Aquáticas", which was being developed in southern Pantanal floodplain, Corumbá, Mato Grosso do Sul, Brazil and was organized by the third author (MEA). This

new species is common in the study area, enabling preliminary observations on its biology.

METHODS

The material examined belongs to the following collections: IBSP, Instituto Butantan, São Paulo (A.D. Brescovit); MCN, Museu de Ciências Naturais, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre (E.H. Buckup); MCTP, Museu de Ciência e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre (A.A. Lise); MNRJ, Museu Nacional do Rio de Janeiro, Rio de Janeiro (A. Kury); ZUFMS, Coleção Zoológica de Referência da UFMS, Universidade Federal de Mato Grosso do Sul, Campo Grande (L.O.I. Souza).

The description format follows Brescovit & Höfer (1994) and the terminology used for the internal structures of the genitalia follows Sierwald (1993, 1996). All measurements are in millimeters. The epigyna were cleared in clove oil to study internal structures. Data on aquatic plant association, web type and prey capture strategies of *Paradosenus corumba* were obtained through field observations of 61 individuals, where 35 were studied by an animal focal method (*sensu* Lehner 1979; total of 175 minutes of observations divided in 35 sessions of five minutes each). These data were collected in temporary ponds in the

southern Pantanal floodplain (between 19°22'–19°33'S and 57°02'–57°03'W) from July 1994–April 1997.

Paradosenus F.O. Pickard-Cambridge

Paradosenus F.O. Pickard-Cambridge 1903: 155, (type species by original designation, *Paradosenus nigricans* F.O. Pickard-Cambridge [= *Dolomedes longipes* Taczanowski 1874]). Sierwald 1993: 55.

Xingusiella Mello-Leitão 1940: 23, (type species by original designation, *X. minima* Mello-Leitão. First synonymized by Sierwald 1993: 55. Carico 1993: 231.

Diagnosis.—*Paradosenus* can be distinguished from other trechaleids by at least four characters, three of which are presumably synapomorphies: male chelicerae with distinct elongated groove leading to the base of fang on the anterior surface of paturon (Figs. 6, 19; Sierwald 1993, fig. 11), leg I extremely long, and presence of a distal tegular projection, not pierced by the duct, in the male palp (Figs. 1, 17, 19; Sierwald 1990, fig. 35; 1993, fig. 12). An additional character would be the presence of slightly to moderately-recurved posterior eye row (Sierwald 1990, figs. 29, 30). The presence of four cheliceral teeth on the retromargin, a character used as diagnostic by Sierwald (1990), was inconsistent. The species included in this work had a retromargin with three teeth (Fig. 12).

Paradosenus corumba Brescovit & Raizer
new species

Figs. 1–6; 11–17; 23

Types.—Male holotype from Corumbá, Mato Grosso do Sul, Brazil, 1994, J. Raizer col., deposited in IBSP 6901; 1♂ & 1♀ paratypes with same data of holotype, deposited in IBSP 6902 and 6903; 1♀ & 4 immatures from Passo do Lontra, Abobral Pantanal sub-region, Corumbá, Mato Grosso do Sul, Brazil, 27 November 1994, J. Raizer col., deposited in IBSP 6904.

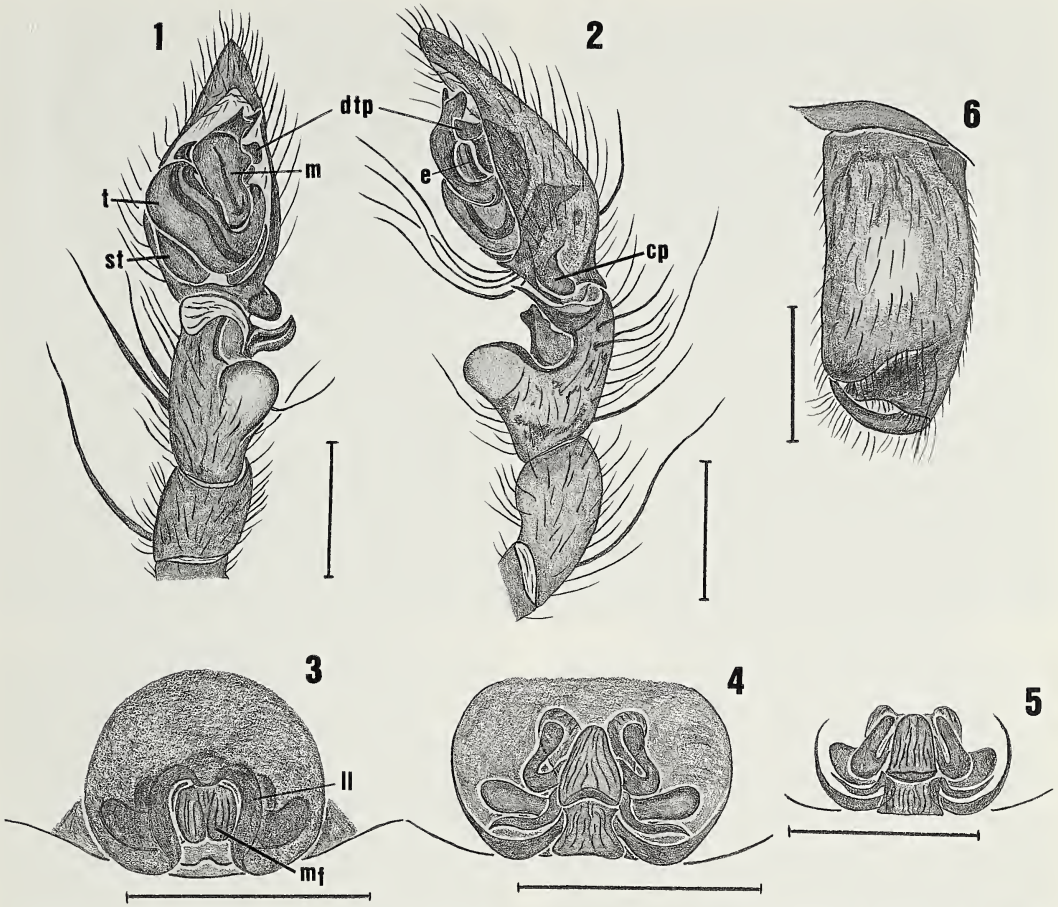
Etymology.—The specific name is a noun in apposition taken from the type locality.

Diagnosis.—The male of *Paradosenus corumba* is distinguished from *P. longipes* (Fig. 13; Sierwald 1990, figs. 34–36) by presence of a retrolateral projection on the base of the cymbium (Figs. 2, 16) and a median apophysis with a bifid distal branch (Figs. 1, 17); the female of *P. corumba* differs from *P. minimus* by the sclerotized internal border of

lateral lobes and middle field with a median depression (Figs. 3, 14).

Description.—*Male:* (holotype). Coloration: carapace orange with grayish border and with brown median dorsal band. Chelicerae yellow. Endites, labium and sternum yellow to white. Legs orange with brown longitudinal bands in all articles. Abdomen orange-brown, dorsally with grayish transversal bands and three pairs of longitudinal white spots. Ventrally shiny white. Total length 2.65. Carapace 1.30 long, 1.20 wide. Clypeus 0.10. Eye diameters and interdistances: AME 0.10, ALE 0.08, PME 0.11, PLE 0.12; AME-AME 0.05, AME-ALE contiguous, PME-PME 0.08, PME-PLE 0.13, ALE-PLE 0.18. MOQ length 0.22, anterior width 0.21, posterior width 0.31. Chelicerae with elongated groove, deep, next to base of fang on the anterior surface (Figs. 6, 11) and 3 promarginal teeth being the median largest and 3 retromarginal denticles (Fig. 12). Labium 0.20 long, 0.17 wide. Sternum 0.75 long, 0.67 wide. Abdomen 1.40 long. Leg measurements: I -femur 2.40; patella 0.70; tibia 2.40; metatarsus 2.40; tarsus 1.00; total 8.90. II -2.00; 0.60; 1.90; 1.90; 0.80; 7.30. III -1.30; 0.40; 0.90; 1.00; 0.35; 3.95. IV -2.10; 0.50; 1.65; 2.10; 0.70; 7.05. Leg spination: tibia I-II v2-2-0; III-IV v2-2-2. Legs with plumose setae (Fig. 15). Bothrium of trichobothria with semicircular rim presenting longitudinal and slender striations (Fig. 13). Palp: retrolateral tibial apophysis subtriangular, very slender at tip; retrolateral ventral projection accentuated and globose (Figs. 1, 16); cymbium with retrolateral basal projection (Figs. 2, 16); tegulum with sperm ducts forming two loops; conductor inconspicuous; median apophysis with two branches, one median rounded and the other distal bifid (Figs. 1, 17).

Female: (IBSP 6904). Coloration as in male except legs with more accentuated bands on the articles and dorsum of abdomen darker. Total length 2.30. Carapace 1.20 long, 1.10 wide. Clypeus 0.07 high. Eye diameters and interdistances: AME 0.10, ALE 0.05, PME 0.12, PLE 0.11; AME-AME 0.03, AME-ALE 0.02, PME-PME 0.06, PME-PLE 0.12, ALE-PLE 0.21. MOQ length 0.23, front width 0.18, back width 0.26. Chelicerae not modified, with 3 promarginal teeth, the second basal being larger than others and 3 large retromarginal teeth. Labium 0.15 long, 0.20 wide.



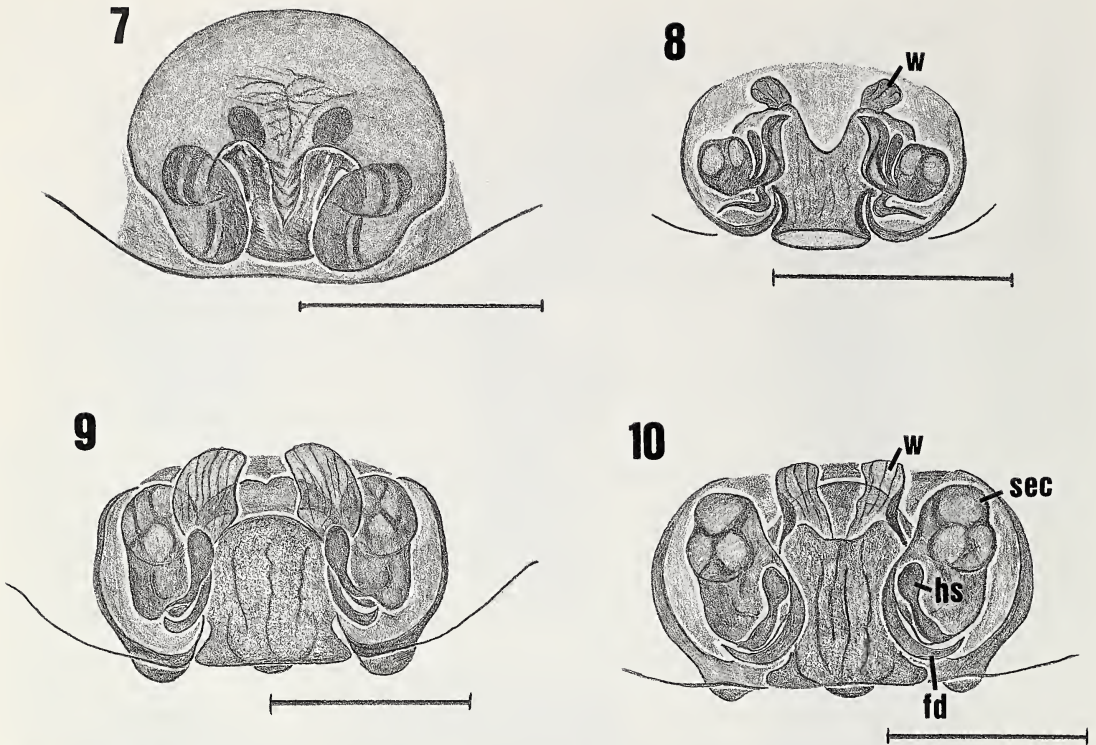
Figures 1-6.—*Paradosenus corumba* new species, male. 1, Left palp, ventral view; 2, Left palp, retrolateral view; 3, Epigynum in ventral view; 4, Epigynum in dorsal view; 5, Epigynum in dorsal view (variation from Porto Cercado, Mato Grosso do Sul); 6, Male chelicera, anterior surface. Abbreviations: cp, basal projection of cymbium; dtp, distal tegular projection; e, embolus; ll, lateral lobes; ma, median apophysis; mf, middle field; st, subtegulum; t, tegulum. Scale bars = 0.25 mm.

Sternum 0.65 long, 0.60 wide. Abdomen 1.30 long. Leg measurements: I -femur 1.50; patella 0.50; tibia 1.40; metatarsus 1.40; tarsus 0.55; total 5.35. II -1.40; 0.50; 1.25; 1.20; 0.50; 4.85. III -1.05; 0.30; 0.70; 0.80; 0.30; 3.15. IV -1.50; 0.45; 1.05; 1.55; 0.50; 5.15. Leg spination as in male. Epigynum: epigynal folds very narrow; middle field short, not covering the epigastric furrow, with an anterior median depression; lateral lobes with narrow border sclerotized and rounded posteriorly (Figs. 3; 14). Vulva: wing of copulatory duct elongated, enlarged distally; true spermathecae slender, curved medially and with rounded head; elongated secondary spermathecae, transversally disposed (Fig. 4).

Variation: Two males: total length 2.65–

2.70; carapace 1.20–1.30; femur I 2.00–2.40. Six females: total length 2.30–3.50; carapace 1.20–1.50; femur I 1.50–2.10. The females from Porto Cercado are darker, and the head of true spermathecae can be very slender (Fig. 5).

Natural history.—*Paradosenus corumba* was observed associated with nine aquatic plants: *Eichhornia azurea* (Sw.) Kunth and *E. crassipes* (Mart.) Solms-Laub. (Pontederiaceae), *Echinodorus paniculatus* Mich. (Alismataceae), *Nymphaea amazonum* Mart. & Zucc. (Nymphaeaceae), *Salvinia auriculata* Aublet (Salviniaceae), *Phyllanthus fluitans* Müll. (Euphorbiaceae), *Panicum mertensii* Roth (Poaceae), *Ludwigia inclinata* (L.f.) Raven (Onagraceae), and *Pistia stratiotes* L. (Ar-



Figures 7-10.—Species of *Paradossenus*, females. 7, 8.—*Paradossenus minimus*. 7, Epigynum in ventral view; 8, Epigynum in dorsal view. 9, 10. *P. longipes*, variation of epigynum in dorsal view. 9. Reserva Florestal Adolfo Ducke, Manaus, Amazonas; 10, São Leopoldo, Rio Grande do Sul. Abbreviations: fd, fertilization duct; hs, head of true spermathecae; sec, secondary spermathecae; w, wing of copulatory duct. Scale bars = 0.25 mm.

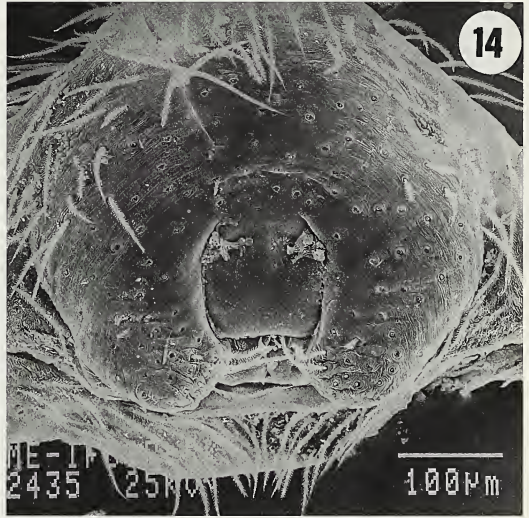
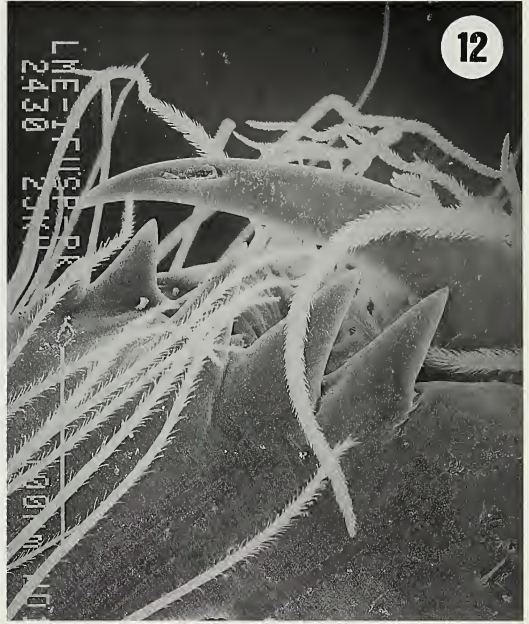
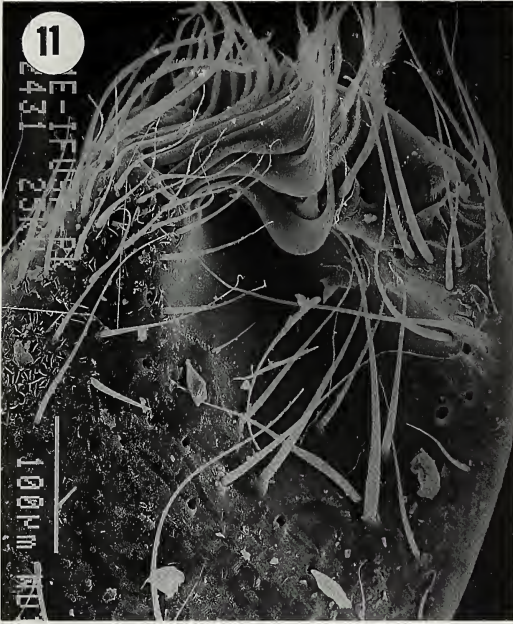
aceae). Spiders were most common in *E. azurea* (45.9% of 61 individuals). On the remaining plants occurrence was lower: 9.84% on *E. crassipes*, 6.56% on *E. paniculatus*, 1.64% on *N. amazonum*, 6.56% on *S. auriculata*, 9.84% on *P. fluitans*, 11.48% on *P. mertensii*, 6.56% on *L. inclinata*, and 1.64% on *P. stratiotes*.

Immatures and adults were found on aerial vegetative parts of the plants, but only immatures were seen in retreats made on damaged or coiled plant leaves. *Paradossenus corumba* adults build irregular, horizontal webs (Fig. 23) which can be simple (observed only on *Echinodorus paniculatus*) or double (on *Eichhornia azurea*, Fig. 23, and *E. crassipes*), in this case without threads connecting the two parts. Spaces were observed between the threads and the plant petiole apex area (see arrows in the Fig. 23). In addition, the web has sticky silk threads. When the web is double, the spider walks under it, surrounding the plant petiole, and passing under each of the

web parts through their spaces. In doing so, the spider is able to inspect the two parts of the web, sequentially.

Some spiders were found walking on a plant or among plants. When walking on the plant, it patrols all its aerial parts. To move from one plant to another, spiders can walk on the water surface or attach silk threads between plant leaves (in tall plants only, *Eichhornia azurea*, *E. crassipes*, *Echinodorus paniculatus* and *Panicum mertensii*).

Paradossenus corumba can capture its prey in two ways. In the first way, a prey (an araneid) was captured actively while *P. corumba* walked on a plant. In this case, the hunting strategy is "search" (*sensu* Alcock 1979). In the second way, when a grasshopper nymph (probably *Cornops* sp., Acrididae) and a Diptera were captured, the spider stayed immobile on the plant leaf, near the water surface, keeping its cephalothorax oriented toward the water, and captured the preys that dropped in front of it. This behavior is characteristic of a



Figures 11–14.—*Paradosenus corumba* new species, male. 11, Chelicerae, anterior surface; 12, Cheliceral teeth; 13, Tarsal trichobothrium, dorsal view; 14, Epigynum of female in ventral view (Scale bars for Figs. 11, 12, 14 = 100μm; Fig. 13 = 1μm).

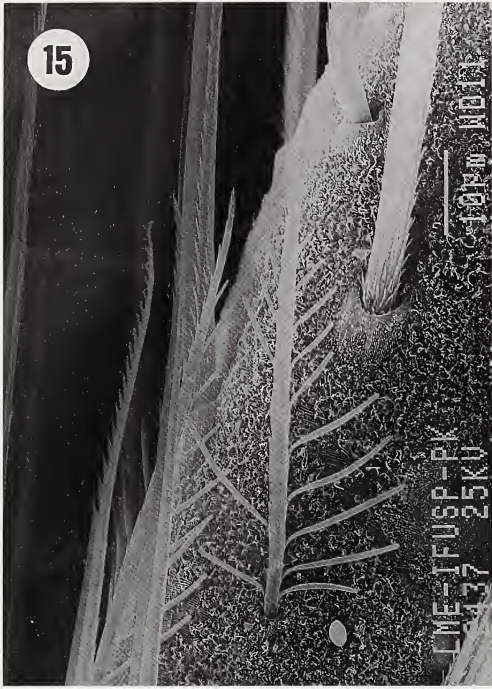
“sit-and-wait” predator (Wise 1993). In both cases, the spider fed on the prey after immobilizing it with a single bite.

The prey capture strategies observed for *P. corumba* indicate versatility in types of prey that are utilized. This versatility is poorly reported for spider species, with the exception of the salticid *Portia fimbriata* (Doleschall 1859) (see Jackson 1982; Jackson & Blest

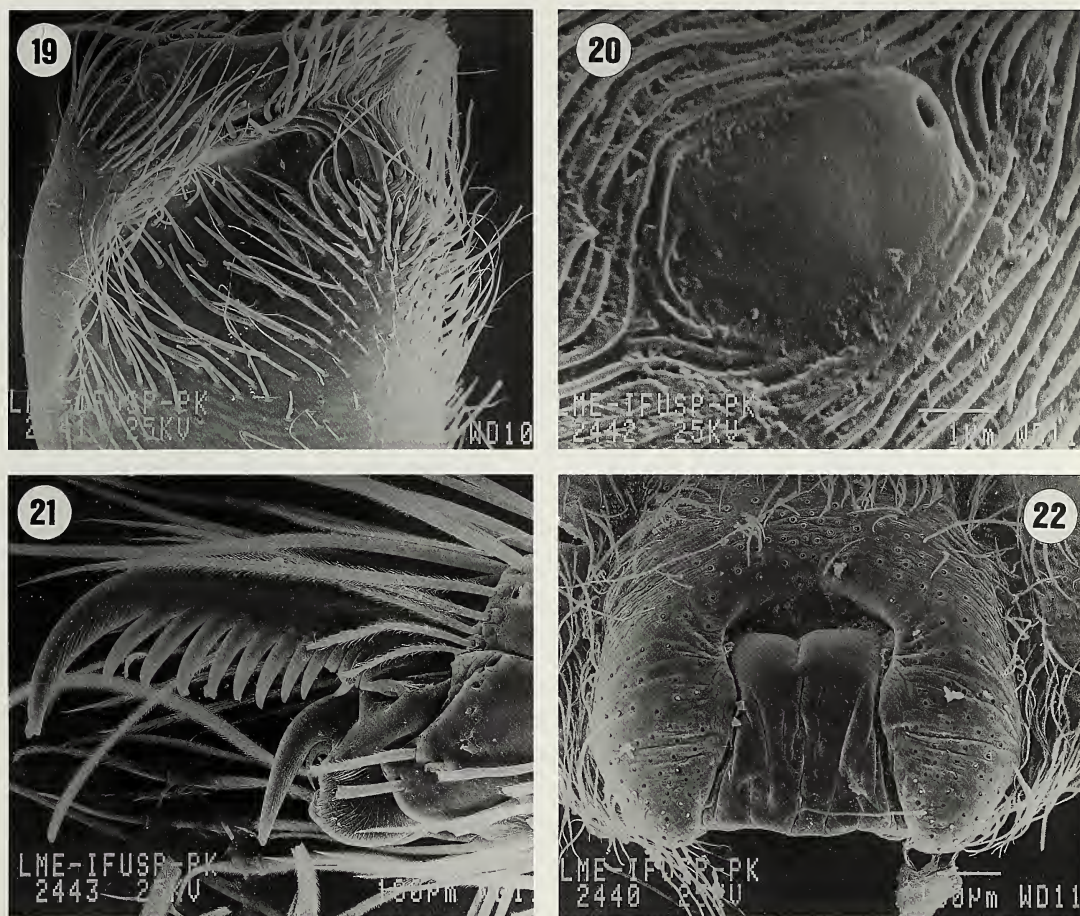
1982) and the araneid *Parawixia bistriata* (Rengger 1836) (see Sandoval 1994).

Distribution.—Mato Grosso do Sul, Brazil.

Material examined.—**BRAZIL.** *Mato Grosso do Sul*: Porto Cercado, 4♀2imm, August 1992 (A.A. Lise & A. Bräul col.) (MCTP 2496; IBSP 6900); Corumbá Abobral sub-region, Passo da Lontra, 2♂1♀3imm, 1996, J. Raizer col. (IBSP 13757-13759; ZUFMS).



Figures 15–18.—Species of *Paradosenus*. 15–17. *Paradosenus corumba*, male. 15, Tibia I, lateral view, plumose setae; 16, Palpal tibia, retrolateral view; 17, Palpal bulb, ventral view. 18, *P. longipes*, male, palpal bulb, ventral view. (Scale bars for Fig. 15 = 10 μ m; Figs. 16–18 = 100 μ m).



Figures 19–22.—*Paradosenus longipes*, male. 19, Chelicerae, anterior surface; 20, Tarsal organ; 21, Leg I, tarsal claws; 22, Epigynum of female from Mato Grosso, in ventral view. (Scale bars for Figs. 19; 21–22 = 100 μ m; Fig. 20 = 1 μ m).

Paradosenus minimus (Mello-Leitão)

Figs. 7, 8

Xingusiella minima Mello-Leitão 1940: 23, fig. 1 (female holotype with egg sac, from Rio Xingu, Pará, Brazil, H. Leonards col., MNRJ 585, examined); Roewer 1954: 144.

Paradosenus minimus: Sierwald 1993: 57.

Diagnosis.—*Paradosenus minimus* is closest to *P. corumba* due to the rounded border of lateral lobes, but may be distinguished by the epigynum with a short and narrow median elevation on the middle field (Fig. 7) and the globose secondary spermathecae (Fig. 8).

Description.—*Female*: (holotype). Coloration: carapace orange to gray (very discolored). Chelicerae red-brown. Endites and labium gray and white at tip. Sternum, legs and pedipalps yellowish. Abdomen dorsally gray-

green, with an anterior dorsal grayish strip and a black band surrounding the spinnerets. Ventrally white. Total length 3.50. Carapace 1.60 long, 1.20 wide. Clypeus 0.12 high. Eye diameters and interdistances: AME 0.08, ALE 0.07, PME 0.12, PLE 0.13; AME-AME 0.05, AME-ALE contiguous, PME-PME 0.12, PME-PL 0.21, ALE-PL 0.27. MOQ length 0.27, front width 0.11, back width 0.37. Chelicerae with 3 promarginal teeth and 3 retromarginal denticles. Sternum 0.85 long, 0.55 wide. Abdomen 1.70 long. Leg measurements: I and II absent. III -femur 1.05; patella 0.35; tibia 0.80; metatarsus 1.00; tarsus 0.40; total 3.60. IV -1.90; 0.50; 1.40; 1.80; 0.65; 6.25. Spination: legs III-IV—tibia v2-2-2. Epigynum: epigynal folds broad, with an anterior widening, rounded; middle field posteriorly

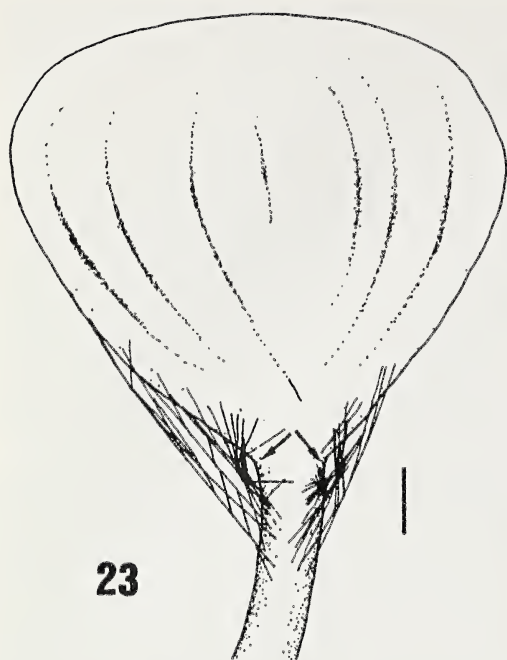


Figure 23.—Typical double web of *Paradosenus corumba* adults, on leaf of *Eichhornia azurea* (Pontederiaceae). Observe the spaces between threads of each web parts and the plant leaf (arrows) used by the spider during the web inspection. Scale bar = 1 cm.

short, with short and narrow median elevation; lateral lobes posteriorly rounded (Fig. 7). Vulva: wing of copulatory duct slightly sclerotized, short and subquadrangular; true spermathecae slender without distinct head; globose secondary spermathecae, without distinct head stalk division (Fig. 8).

Natural history.—The egg sac, reported by Mello-Leitão (1940) as globose, is similar to those found in the Lycosidae, attached to spinnerets. Also present, as in *P. longipes*, are two discs, the upper larger than the lower disc, vault shaped, with the central scar where it was attached to spinnerets, the lower disk smaller and flat, with 20–25 shiny round eggs.

Distribution.—North of Mato Grosso, Brazil.

Material examined.—Only the type.

Paradosenus longipes (Taczanowski)

Figs. 9, 10; 18–22

Dolomedes longipes Taczanowski 1874: 88 (♀ lectotype and ♂ paralectotype, “Polska Academy of Sciences”, designated by Sierwald (1993), of

Cayena, 04°055'N, 52°18'W, Depto Cayena, Guiana Francesa, K. Jelski col., not examined).

Paradosenus nigricans Pickard-Cambridge 1903: 155 (male holotype and female paratype, “The Natural History, British Museum” BMNH-1898.5.5.101-2, from Buyassu, Paraná e Breves, Maranhão, Brazil, not examined); Roewer 1954: 139; Bonnet 1958: 3325; Caporiacco 1948: 630; Sierwald 1990: 35; 1993: 59 (syn.).

Paradosenus longipes: Caporiacco 1948: 630.

Paradosenus taczanowskii Caporiacco 1948: 631 (2♂ syntypes, “Museo di Zoologia di Specola, Firenze”, from Two Mouths, Essequibo, Guiana and Tibicuri-Cuyaha, Demerara, Guiana, not examined); Sierwald 1990: 35.

Morphological notes.—Chelicerae in Fig. 19 showing the distinct elongated groove; tarsal claws long, bearing 11–12 teeth, inferior tarsal claw on short tarsal onychium with slender ridges and presenting an elongated tooth (Fig. 21); tarsal organ oval with small and circular opening (Fig. 20). Copulatory organs: no variation was found in the male palp collected in the northern region of South America (see Sierwald 1990, fig. 34) and those collected from the south of Brazil (Fig. 18). Among the females, no variation was found in the external plate of the epigynum (Fig. 22), but examining the internal structures, significant variation was detected in the form of the wings of copulatory ducts, which are very enlarged in the females from Manaus, Amazonas (Fig. 9) and narrowed in the females from Rio Grande do Sul (Fig. 10). Despite these variations we consider all specimens as *P. longipes*.

Distribution.—Previously known from Venezuela, Guiana, Colombia, Bolivia, Peru and north of Brazil (Sierwald 1993: 62, 63). The new records extend the range of this species to south of Brazil and north of Argentina.

New records.—**BRAZIL.** *Acre*: Serra do Divisor National Park (Camp), 1♀, 14 November 1996 (R.S. Vieira col.) (IBSP 9305); *Amazonas*: Manaus, Reserva Florestal Adolfo Ducke, 1♂, 8 August 1992 (S. Darwich col.) (MCTP 2846); 1♀, 8 April 1992 (S. Darwich col.) (MCTP 2718); 1♀, 8 April 1992 (U. Barbosa col.) (MCTP 2719); *Mato Grosso*: Confluency Rivers Koluene and Xingu, 1♂3♀ (J.C. Carvalho col.) (MNRJ 13446; IBSP 13756); *Bahia*: Iraquara, Pratinha (23°11'S, 48°12'W), 2 ♀, 5 May 1998 (L.S. Rocha col.) (IBSP 20781); *São Paulo*: Mogi das Cruzes, Rio Tietê, 1♀, July–August 1997 (R. Martins col.) (IBSP 11970); *Paraná*: Candói/Mangueirinha, Reservatório do Rio Jordão,

Usina Hidrelétrica de Segredo, 1♀, 29 April 1996 (A.F. Moraes & M.L. Javorowski col.) (IBSP 7142); Dois Vizinhos/Cruzeiro do Iguaçu, Foz do Chopin, 1♀, 8–15 November 1998 (Eq. IBSP col.) (IBSP 21247); *Rio Grande do Sul*: Rio Uruguai (Rodovia BR 153), 1♂, February 1989 (Eq. PUC col.) (MCTP 1296); São Leopoldo, 1♀, 25 March 1983 (C.J. Becker col.) (MCN 11518); Triunfo, 1♀ with egg sac, 12 January 1989 (H.A. Gastal col.) (MCN 18086); **ARGENTINA**. *Entre Misiones e Corrientes*: 1♀, 03–12 January 1989 (Eq. Garabi col.) (MCTP 1289).

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OPTICAL STRUCTURE OF THE CRAB SPIDER *MISUMENOPS PALLENS* (ARANEAE, THOMISIDAE)

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ABSTRACT. We describe the histological structure of the eyes of *Misumenops pallens* (Araneae, Thomisidae). We have carried out frontal, sagittal and transverse histological sections of the eyes. All the eyes have cuticular and laminar corneas and lenses. The anterior median eyes have two cellular types in the rhabdom; the remaining eyes have three cellular types. The anterior median eyes have a dark pigmented U-shaped mark in the middle of the retina. The indirect eyes have a dark pigmented band divided by a grate tapetum. The pathway of the optic nerves is also described. Our results suggest that Thomisidae may be a close relative of the superfamily Lycosoidea.

RESUMEN. Se describe la estructura histológica de los ojos de *Misumenops pallens* (Araneae, Thomisidae). Se realizaron cortes de los ojos en sección frontal, sagittal y transversal. Todos los ojos tienen córneas y lentes cuticulares y laminares. Los ojos medios anteriores tienen dos tipos celulares en el rhabdoma mientras que los restantes ojos tienen tres tipos celulares. Los ojos medios anteriores poseen, en el centro de la retina, una mancha de pigmento oscuro en forma de U. Los ojos de visión indirecta tienen una banda oscura de pigmento dividida por un tapete de tipo "grate." Se estudia también el recorrido de los nervios ópticos. Nuestros resultados sugieren que Thomisidae puede estar relacionado con la superfamilia Lycosoidea.

Keywords: Eyes, optic nerves, phylogenetic relationship

Misumenops pallens (Keyserling 1880) (Thomisidae) are spiders that normally inhabit flowers and capture their prey by ambush. Their eyes are arranged in two recurved rows; in the anterior row the anterior median eyes (AME) are next to the bigger anterior lateral eyes (ALE) (Fig. 1). The posterior row eyes are equidistant, the posterior median eyes (PME) being smaller than the posterior lateral eyes (PLE). Lateral eyes are located on prominent tubercles. The dioptical apparatus of all the eyes of *Misumenops pallens* is formed by a cuticular cornea, a laminar lens and the "vitreous body," constituted by cone cells arranged in a unique stratum that rests against a basal membrane. The eyes of *Misumenops* sp. have a dark pigmented ring called the "pupil," a character shared with Lycosidae (Hermann 1971). The tapetum of the secondary eyes of Thomisidae is difficult to observe (see Levi 1982). In this study, the optic structure of *Misumenops pallens* is described in order to pro-

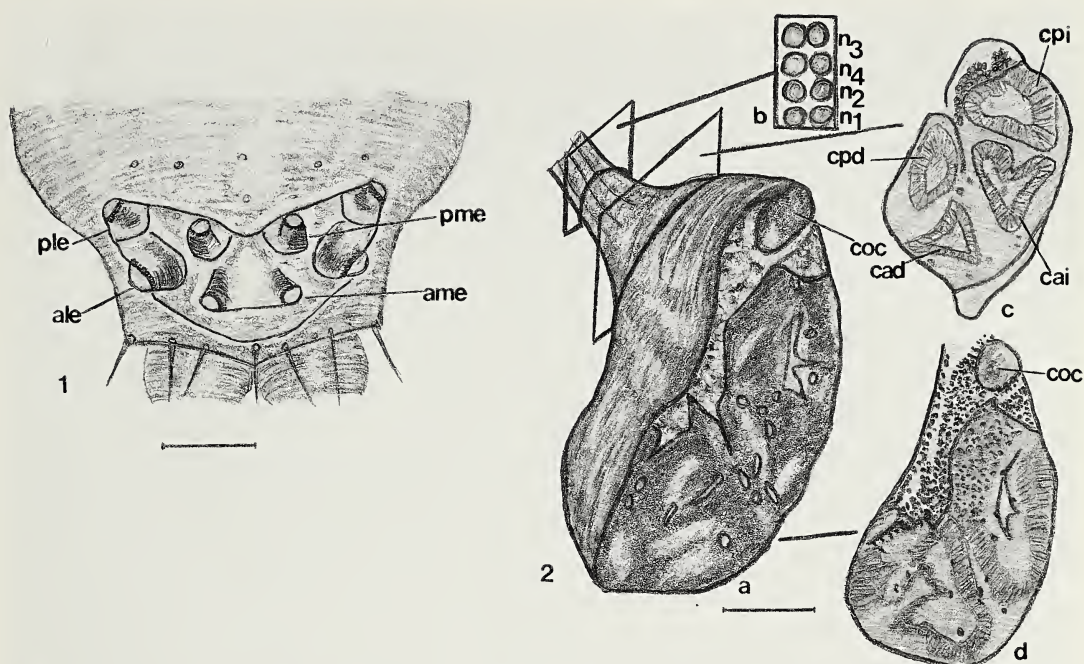
vide new morphological characters that can be used in phylogenetic studies.

METHODS

Six adult females of *Misumenops pallens*, collected in March 1995 on soybean flowers in Burruyacu department (Tucumán, Argentina), were studied. Voucher specimens and histological slides are deposited in the arachnid collection of Fundación Miguel Lillo, Tucumán, Argentina (lot FML N° 2203). The spiders were anesthetized with chloroform. The cephalic regions of these spiders were dissected and were fixed in Bouin. The material was kept in n-Butyl alcohol during the time required to soften the cuticle, prior to embedding in Paraplast.

Serial sections of 6 μ m thickness were cut, following the frontal, transverse and sagittal planes. Preparations were stained with Mallory-(Azan) Heidenhain and Haematoxylin-Eosin.

Diagrams of optic nerves were prepared to



Figures 1, 2.—*Misumenops pallens*. 1. Ocular disposition; 2. Diagram showing the union of the ocular nerves in the cerebral ganglion —a. General view of the cerebral ganglion showing optic center, b. Transverse section showing the distribution of the optic nerves before their union with the cerebral ganglion, c. Transverse section showing the four optic centers, d. Transverse section of the optic center formed by the fusion of the four centers. *Abbreviations*: ale = anterior lateral eyes; ame = anterior median eyes; cad = anterior right optic center; cai = anterior left optic center; co = optic center; coc = optic center of cerebral ganglion; cpd = posterior right optic center; cpi = posterior left optic center; n₁ = optic nerve of anterior median eye; n₂ = optic nerve of anterior lateral eye; n₃ = optic nerve of posterior median eye; n₄ = optic nerve of posterior lateral eye. *Scale bars*: Fig. 1 = 0.42 mm; Fig. 2 = 66 μ m.

trace their course as they leave each eye and enter the optic center of the cerebral ganglion; the nerves of each eye are designated as follows: n₁ (AME), n₂ (ALE), n₃ (PME) and n₄ (PLE).

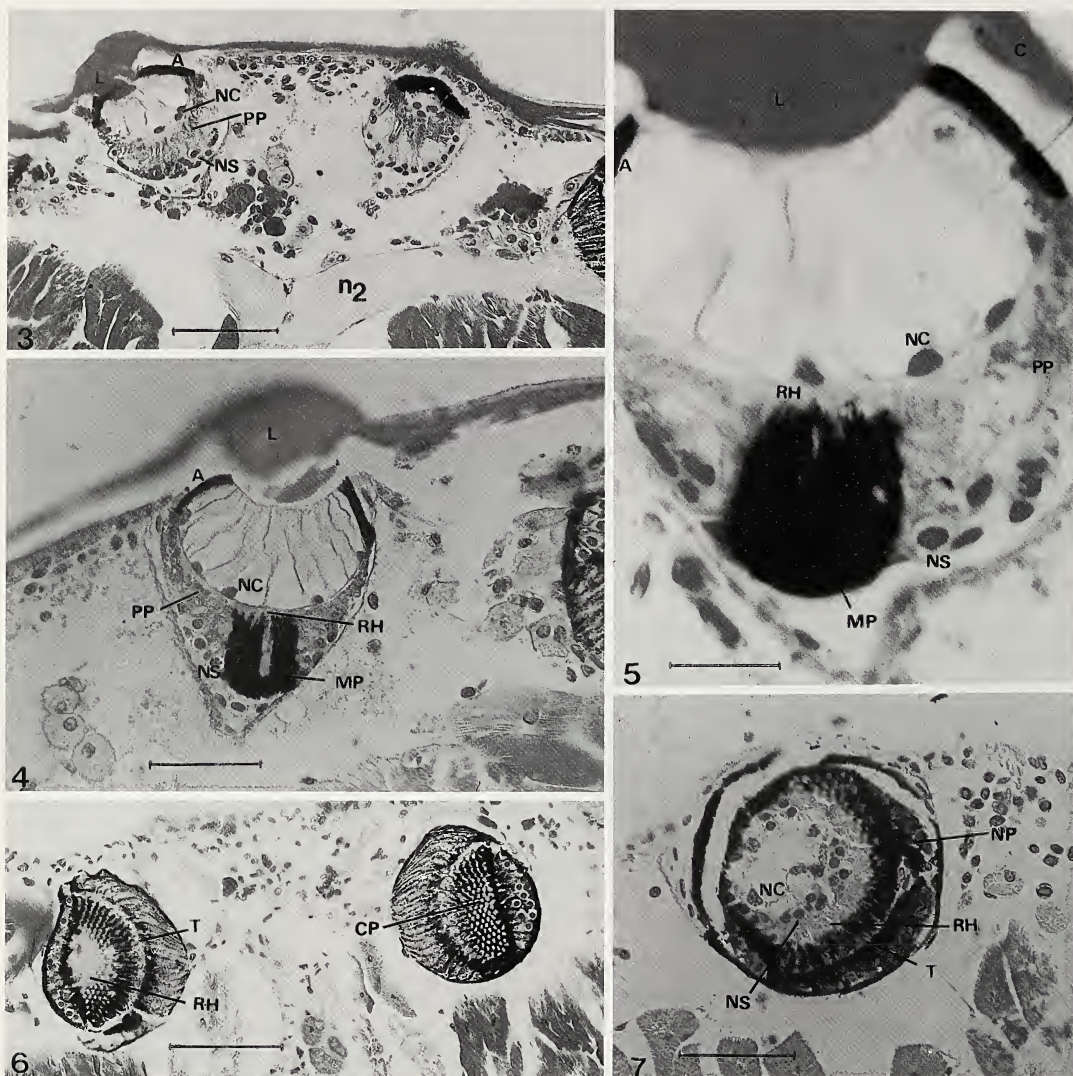
RESULTS

Anterior median eyes (AME).—(Figs. 3–5). These eyes are pyriform, with their vertex towards the inner part. They have a cuticular and laminar cornea, with the outer surface formed by overlapping plates, separated by complete transverse grooves. The lens, located beneath the cornea, is laminar, ogival, with the greater convexity towards the inner part of the eye (Figs. 3, 5). It has few transverse grooves. Cone cells (Eakin & Brandenburger 1971) lie below the lens and contain a few irregular basal nuclei with homogeneous granular chromatin (Figs. 4, 5). Cone cells are arranged in only one stratum and send out projections towards the lens. Cone cells rest against a thin

basal membrane that separates them from the retina (Fig. 4). There is a wide dark pigmented ring (the “pupil”) in the anterior portion of the vitreous body (Figs. 4, 5).

The retina is sub-conical and is formed by two cellular types, pigmented supporting cells and sensitive cells. Pigmented supporting cells are distributed in the central region of the rhabdom forming a U-shaped spot of dark pigment. There is a calyx-shaped layer of brown pigment between this spot and the pigmented ring of the dioptical apparatus (Figs. 4, 5). The pigmented layer is constituted by granules of brown and black pigment. Brown pigment disposition is similar to the location of the dark pigment in the secondary eyes, while black pigment is located only in the central pigmented zone of the retina. The function of each type of pigment has yet to be established.

Each sensitive cell consists of a distal portion below the basal membrane, that forms a thin rhabdom located only in the central por-

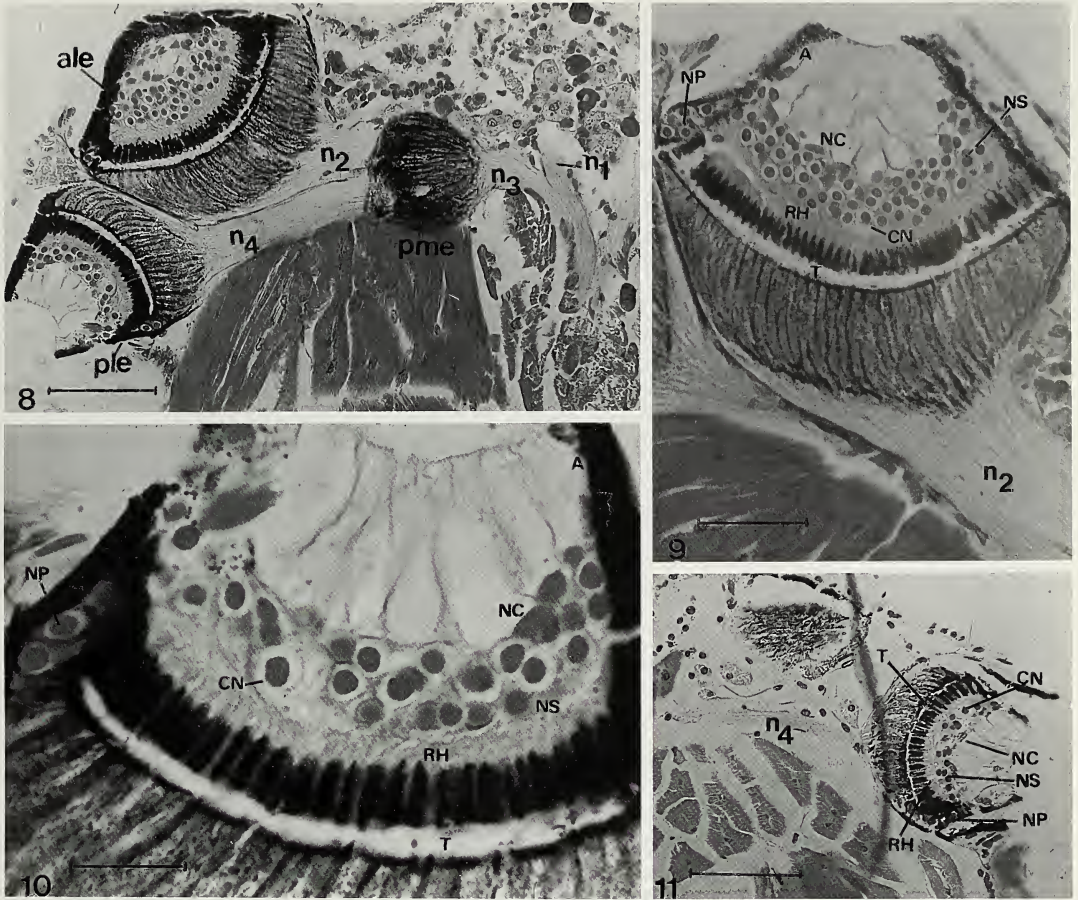


Figures 3–7.—*Misumenops pallens*. 3–5. Anterior median eyes (AME); 3. Frontal section showing arrangement (250 \times); 4. Frontal section showing structural elements (400 \times); 5. Frontal section showing details of rhabdomeres and nuclei of sensitive cells (1000 \times). 6–7. Posterior median eyes; 6. Frontal section showing tapetum (250 \times); 7. Frontal sections showing structural elements (400 \times). *Abbreviations*: A = pigmented ring; C = cornea; CP = pigmented supporting cell; L = lens; MP = pigmented spot; NC = nucleus of cone cell; NS = nucleus of sensitive cell; n_2 = optic nerve of lateral anterior eyes; NP = nucleus of pigmented supporting cell; PP = brown pigment; RH = rhabdomeres; T = tapetum. *Scale bars*: Fig. 3 = 60 μ m, Fig. 4 = 4 μ m, Fig. 5 = 1.6 μ m, Fig. 6 = 66 μ m and Fig. 7 = 42.6 μ m.

tion in front of the central pigmented spot (Fig. 5). The intermediate segment of the sensitive cells crosses the pigmented layer and ends in the nuclear portion, where the cell increases its volume (Fig. 5). The nuclei of sensitive cells are irregular, with homogeneous granular chromatin. They are located in a peripheral basal stratum (Fig. 4).

Anterior lateral eyes (ALE).—(Fig. 9).

These eyes are conical and situated in an antero-lateral position. Cornea, lens and cone cells are similar to those of the AME. The retina is formed by three cellular types, sensitive cells, pigmented supporting cells, and non-pigmented supporting cells (Fig. 9). Sensitive cells are arranged in at least two or three strata. They contain rounded nuclei, with granular chromatin homogeneously distrib-



Figures 8–11.—*Misumenops pallens*. 8. Arrangement of posterior eyes and lateral anterior eyes, frontal section, showing disposition of optic nerves (250×); 9. Lateral anterior eyes showing principal structures (400×); 10–11. Lateral posterior eye; 10. Posterior lateral eye showing non-pigmented supporting cells (1000×); 11. Posterior lateral eyes showing optic nerve and structural elements (250×). *Abbreviations:* ale = anterior lateral eye; pme = posterior median eye; ple = posterior lateral eye; A = ring (“pupil”); CN = non-pigmented supporting cell; NC = nucleus of cone cell; NP = nucleus of pigmented supporting cell; NS = nucleus of sensitive cell; n₁ = optic nerve of anterior median eye; n₂ = optic nerve of anterior lateral eye; n₃ = optic nerve of posterior median eye; n₄ = optic nerve of posterior lateral eye; RT = rhabdomeres; T = tapetum. *Scale bars:* Figs. 8 and 11 = 66 μm; Fig. 9 = 42.6 μm; Fig. 10 = 15 μm.

ed, and clear cytoplasm around the nucleus. The intermediate segment extends from the soma of sensitive cells and continues in the parallel rhabdomeres (Fig. 9), whose projections cross the “RT” type tapetum (according to Homann 1971) (Fig. 9). The few non-pigmented supporting cells are large and have ovoid nuclei with homogeneous granular chromatin. They have abundant clear cytoplasm with projections that can cross the rhabdomere layer (Fig. 9). Pigmented supporting cells contain cytoplasm with a great number of granules of concentrated pigment arranged in a dark layer. They are located between the

rhabdomeres and the tapetum, and extend forward enclosing the vitreous body up to the lens base. There is a less pigmented wide layer below the tapetum. It is difficult to observe the nuclei of these cells due to the great amount of pigment, except in the peripheral lateral zone, where groups of nuclei of these cells can be observed (Fig. 9).

Posterior median eyes (PME).—(Figs. 6, 7). These rounded eyes are located in a dorso-lateral position. Cornea, lens and cone cells are similar to those of the AME. Retina cells are similar to those of the ALE, except that the nuclei of sensitive cells are arranged in

two strata. Non-pigmented supporting cells are rare; they possess pyriform nuclei with homogeneous granular chromatin and small cytoplasm projections between the rhabdomeres. There are two layers of pigmented supporting cells, as in the ALE. These cells are separated by a well-developed "RT" type tapetum (Fig. 6). In a transverse section, rounded nuclei are visible, with homogeneous granular chromatin and some peripheral clear cytoplasm (Fig. 7).

Posterior lateral eyes (PLE).—(Figs. 10, 11). These eyes are conical eyes and have cornea, lens and cone cells that are similar to those of the AME. The retina is similar to the retina of the ALE, except the nuclei of the sensitive cells are arranged in at least three strata. Pigmented cells, non-pigmented cells and shape of the tapetum are similar to those of the ALE (Figs. 10, 11).

Trajectory of optic nerves.—Optic nerves from the AME run independently and parallel as they leave each eye, following the prosomal median line (Fig. 12). The rest of the nerves emerge from the corresponding eyes, curve and run paired along the body median line (Fig. 13), between the poison glands.

At the median region of the prosoma optic nerves remain paired. Their arrangement from the ventral to the dorsal part of the body is: n_1 , n_2 , n_4 and n_3 (Figs. 2b, 8). Posteriorly, optic nerves fuse to form four optic centers (Figs. 2c, 14). The two ventral optic centers correspond to the fusion of n_1 and n_2 of their respective sides, while the dorsal optic centers, right and left, are formed by the fusion of the corresponding n_4 and n_3 . The four optic centers fuse in the posterior region of the prosoma in a dorsal optic center located in the cerebral ganglion (Figs. 2d, 15).

DISCUSSION

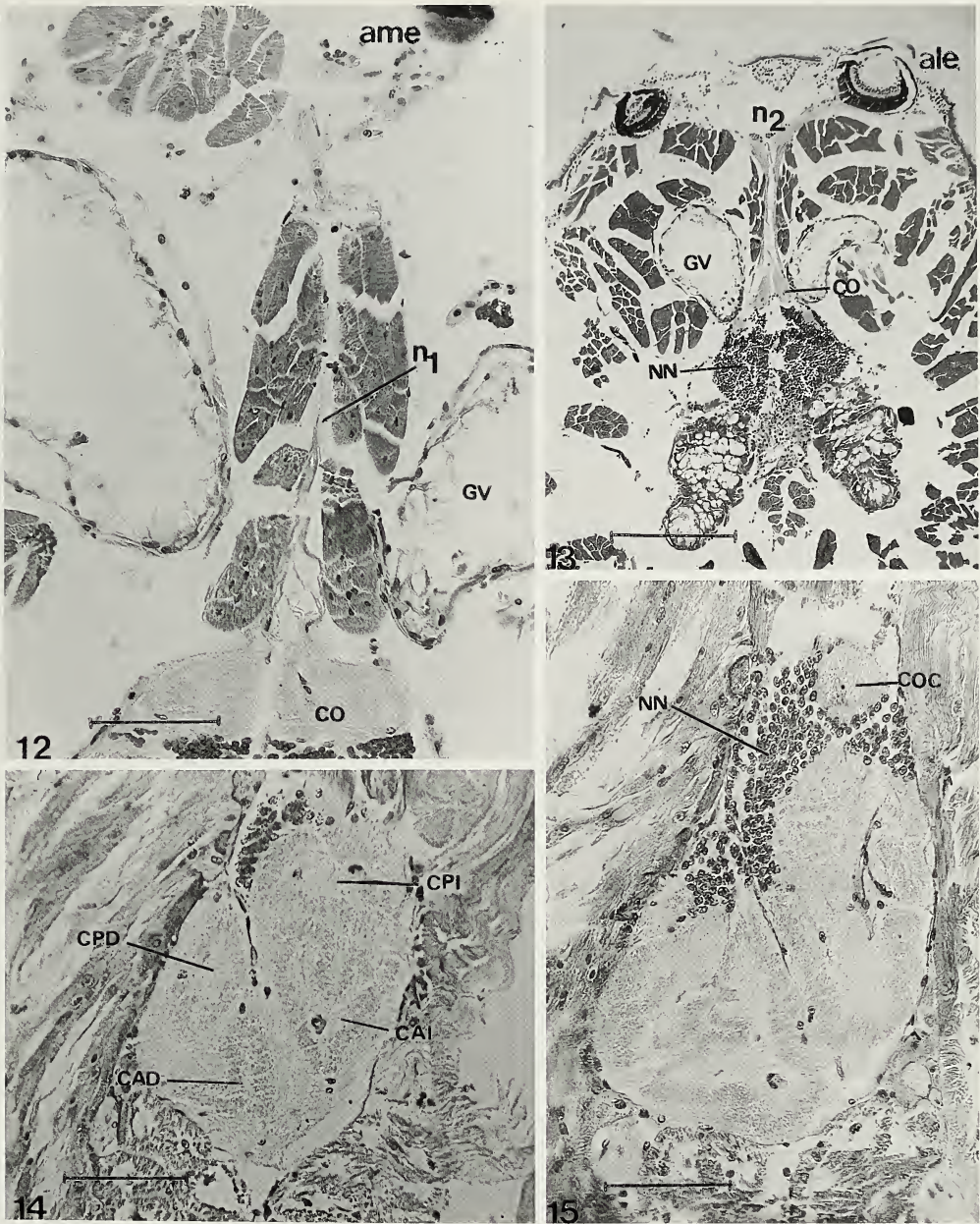
Different cellular types were observed in the ocular structure of *Misumenops pallens*. This agrees with Eakin & Brandenburger's (1971) description for Salticidae, Melamed & Trujillo Cenóz's (1966) for Lycosidae and Corronca & Terán's (1997) for *Selenops* Latreille (Selenopidae). However, the similarities found in the cellular types of the eyes of these families of spiders do not imply that there are no differences in their general structure.

The tapetum and the anatomical structure of eyes are characters that can be used to reconstruct the phylogenetic relationships of spi-

ders. Homann (1971) mentioned the presence of the "pupil" and the tapetum type as among the characters shared by both the Thomisidae and Lycosidae. Homann (1975) considered Thomisidae as sister group of the monophyletic group Lycosoidea (Lycosidae, Senoculidae and Oxyopidae). Levi (1982) placed Thomisidae in their own superfamily together with Aphantochilidae, while Coddington & Levi (1991) considered Thomisidae in the Dionycha, even when its placement is not very clearly established. Philodromidae, Heteropodidae and Selenopidae could be considered as groups related with Thomisidae, because of the presence of laterigrad legs and the locomotion type (Coddington & Levi 1991). Griswold (1993) studied the phylogenetic relationships of Lycosoidea and considered the copious and diverse anatomical and morphological characters, and established that the presence of an RT type of tapetum in at least one of the eyes is one of the two synapomorphies that supports the monophyly of this superfamily. The same author considered that the possible homology of the tapetum shape is the only evidence to include this family within Lycosoidea. Corronca & Terán (1997) suggested the probable relationship of Selenopidae with Lycosoidea. Results obtained from the study of the ocular structure of *Misumenops pallens*, and extrapolated to the rest of Thomisidae, show the existence of certain anatomical characters (presence of a well developed RT type tapetum in all secondary eyes, except in PME where is reduced, and the "pupil") shared with Lycosidae and of others (RT tapetum and sensitive cells in the secondary eyes arranged in at least two strata) with Selenopidae. These affinities suggest the probable relationship of both families (Thomisidae and Selenopidae) with Lycosoidea.

The U-shaped spot of dark pigment, located in the central portion of AME retina in Thomisidae, could be homologous with the V-shaped pigmented spot, typical of AME of Salticidae. Both structures present the same topology, but the four layers of receptive segments that have been described by Eakin & Brandenburger (1971) for Salticidae are not present in Thomisidae.

Recent observations by De la Serna & Spinelli (1995) for *Latrodectus* species (Theridiidae) show that the four optic centers fuse to-



Figures 12–15.—*Misumenops pallens*. 12. Connection between anterior median eyes into the cerebral ganglion (250×); 13. Pathway of optic nerves of the anterior lateral eyes until fusion with the optic center, frontal section (160×); 14. Four optic centers, transverse section in the middle portion of the prosoma (250×); 15. Optic center formed by the fusion of the four centers, transverse section to the posterior portion of the prosoma (250×). Abbreviations: ame = anterior median eyes; ale = anterior lateral eye; CAD = anterior right optic center; CAI = anterior left optic center; CO = optic center; COC = optic center of cerebral ganglion; CPD = posterior right optic center; CPI = posterior left optic center; GV = venom gland; NN = neuronal nucleus; n₁, optic nerve of anterior median eye; n₂ = optic nerve of anterior lateral eye. Scale bars: Figs. 12, 14 and 15 = 66 μm, Fig. 13 = 94.2 μm.

gether in an unique optic center in the cerebral ganglion. Our study of the trajectory of the optic nerves in *Misumenops pallens* agrees with these authors; however, the nerves do not fuse in their trajectory until they form the first optic centers. The presence of this character in Lycosidae and Salticidae should be studied.

ACKNOWLEDGMENTS

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MALE DIMORPHISM IN *OEDOTHORAX GIBBOSUS* (ARANEAE, LINYPHIIDAE): A MORPHOMETRIC ANALYSIS

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ABSTRACT. The linyphiid spiders *Oedothorax gibbosus* (Blackwall 1841) and *Oedothorax tuberosus* (Blackwall 1841) were formerly described as separate species due to marked differences in prosomal structures of the males. During the last decade it was demonstrated that they are two forms of a single species. However, it remained to be shown whether the former species represent two distinct morphs or extremes of a continuum of variation. A morphometric examination of 246 alcohol-preserved specimens revealed that individual spiders can clearly be assigned to one of two forms. No intermediates were found, demonstrating that there are two distinct morphs.

Keywords: Species status, polymorphism, morphometry, sexual selection, gustatorial courtship

Why individuals of some species occur in distinct varieties has been of considerable interest to evolutionary biologist (e.g., Clarke 1962). Dimorphism represents the simplest case of polymorphism, with two varieties maintained within the population. The most common case of dimorphism is the sexual dimorphism with males and females showing dimorphism in size (Anderson 1994). Behavioral or morphological dimorphism in one sex, usually occurring in the male sex, is known for a relatively large number of insects (Hamilton 1979; Thornhill & Alcock 1983; Danforth 1991; Alcock 1996; Eberhard & Gutiérrez 1991). To our knowledge, the only spider species investigated to date is the jumping spider, *Maevia inclemens* (Walckenaer 1837), in which the morphs show striking differences in body color and courtship behavior (Clark & Uetz 1992, 1993). Species with dimorphic males provide a unique opportunity to address questions about the importance of female choice (Gadgil 1972; Clark & Uetz 1992), male-male competition (Danforth 1991; Eberhard & Gutiérrez 1991), sensory exploitation (Clark & Uetz 1993), and alternative mating tactics with equal or unequal fitness (Austad 1984; Dominey 1984). However, it has yet to be shown that the varieties under consideration result from the expression of different developmental programs with a bimodal distribution, excluding the differences that are simply extremes of a continuum of variation.

The linyphiid spiders *Oedothorax gibbosus*

(Blackwall 1841) and *Oedothorax tuberosus* (Blackwall 1841) were described as separate species due to differences in prosomal structures of the males. In *O. gibbosus*, the male prosoma is raised to form a marked protuberance in front of which lays a deep notch surrounded by long black hairs. Protuberances, notches, grooves and poreplates frequently found in male linyphiid spiders were shown to function as gustatorial courtship devices in several species (Lopez & Emerit 1981; Schaible et al. 1986; Schaible & Gack 1987). Males of *O. tuberosus* on the other hand, lack the marked protuberance, notch and hair. However, the division was doubted by several authors (Simon 1926; Locket & Millidge 1953; Wiehle 1960; Bosmans 1985; Roberts 1987) as neither the male pedipalps can be distinguished nor are there differences in female somatic and genitalic characteristics. Moreover, the two species almost always occur syntopically (Wiehle 1960; Roberts 1987; Maelfait et al. 1990). Roberts (1987) strengthened this view by stating that: "occasional specimens seem to represent an almost intermediate state" and by including a drawing of a tuberosus male with a slight notch. Not until a rearing study was undertaken by De Keer & Maelfait (1988) in which both male forms were reared from one egg-sac was it shown that *O. gibbosus* and *O. tuberosus* are two forms of one species. A more detailed rearing study supported this finding, demonstrating that the two forms are very likely determined

by one major gene with a dominant and a recessive allele where the tuberosus phenotype is expressed in individuals carrying homozygotic recessive alleles (Maelfait et al. 1990). From this genetic system follows that the two forms must be discrete morphs which is incompatible with the supposed intermediate forms. In a morphometric analysis, we examine whether the *gibbosus* and *tuberosus* forms can be clearly distinguished on morphological grounds. This study provides the basis for the following investigations on female mate choice.

METHODS

Oedothorax gibbosus occurs in North-, West- and Central Europe (Wiehle 1960). It is restricted to low productive, wet grassland and marshes that are frequently flooded during winter and requires high water quality, resulting in a rather patchy distribution (De Keer & Maelfait 1989).

We examined 246 alcohol-preserved specimens from the Institut Royal des Science Naturelles de Belgique, Bruxelles, captured in pitfall traps from 1977 to 1991 at different locations in Belgium. We chose this collection for two reasons, 1) the most detailed study on the species was conducted in Belgium by Maelfait et al. (1990), and 2) this collection proved to be the largest one available, a prerequisite for a solid morphometric investigation.

An example of each male form is illustrated in Figs. 1–4. For the morphometric analysis we took the following measures (in μm) (Figs. 5–8): length of patella plus tibia of the first leg (a), height of the prosoma (b), width of the prosoma (c), length of the prosoma (d), dorsal line along the prosoma, when viewed from the side (e) and depth of the notch (f). To measure the height a perpendicular line was drawn from the highest point of the prosoma. The dorsal line is a measure that includes size and dimension of the notch and the hump. The height of the prosoma and the depth of the notch were measured additionally to examine both structures separately. The depth of the notch was measured by drawing a straight line over the notch from which a perpendicular was drawn to the deepest point of the notch. The width of the prosoma was measured at the widest part of the prosoma. To measure prosoma length, the length of a

straight line from the front to the back of the prosoma, parallel to the sternum, was taken. The measure of patella plus tibia is frequently used as a measure of leg size and served as a measure independent of prosomal size.

The measures were taken with a macroscope (WILD M420) fitted with a CCD-camera (Pieper FK 5062), connected to a computer provided with the program NIH-Image (Version 1.60b7). SEM investigations were performed with a Hitachi S2460N using unsputtered alcohol material under low vacuum mode.

All statistical analyses were performed using SPSS for Windows95, Version 8.0.1. The level of significance was set at 0.05.

RESULTS

The data were tested for normal distribution: prosomal length, prosomal width, prosomal height and length of the first leg showed a normal distribution (Kolmogorov-Smirnov-one-sample-test: $n = 246$, (leg 1: $n = 243$), in all cases $P > 0.05$). The dorsal line of the prosoma ($n = 246$) and the depth of the notch ($n = 219$) were not normally distributed (K-S test, both $P < 0.01$).

In Principal Component Analysis using a correlation matrix and varimax rotation, two principal components with eigenvalues greater than 1 were extracted (Table 1). A clear separation of the two morphs was possible along PC1 which explains 48% of the variance. Characters highly correlated with this component are the dorsal line, the height of the prosoma and the depth of the notch, all characters whose presence is attributed to the *gibbosus* form (Figs. 1, 2). The scatterplot of PC-scores shows two distinct distributions (Fig. 9), the left cloud representing the *tuberosus* form and the right one the *gibbosus* form. No intermediate forms were found.

The character length of the dorsal line along the prosoma incorporates several prosomal measures. In order to exclude size effects, we used an index of the dorsal line relative to size as measured by prosoma length. The resulting histogram (Fig. 10) shows a clear bimodal distribution and confirms that there are no intermediate forms. Thus we can safely assume the existence of two distinct morphs in *O. gibbosus*.

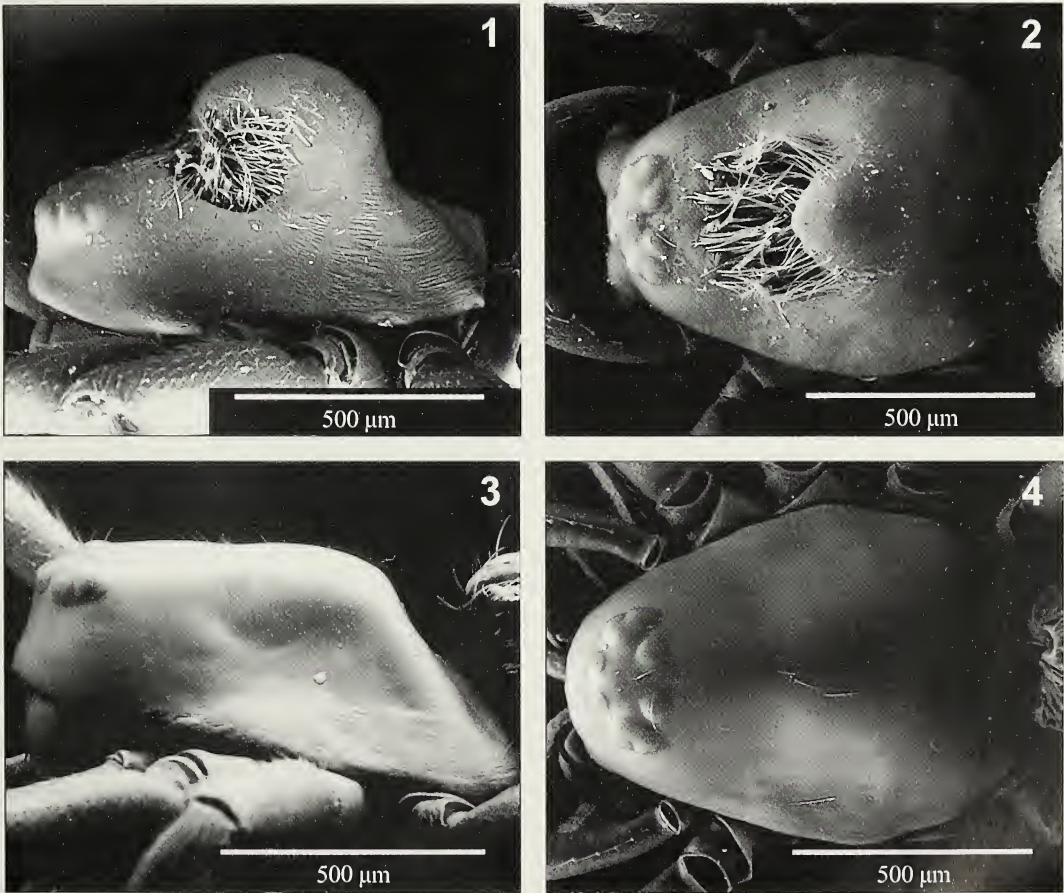
The mean of the dorsal line along the prosoma of the *gibbosus* morph ($\bar{x} = 1948 \mu\text{m}$,

Table 1.—Rotated component matrix resulting from Principal Component Analysis using eigenvalues greater than 1.

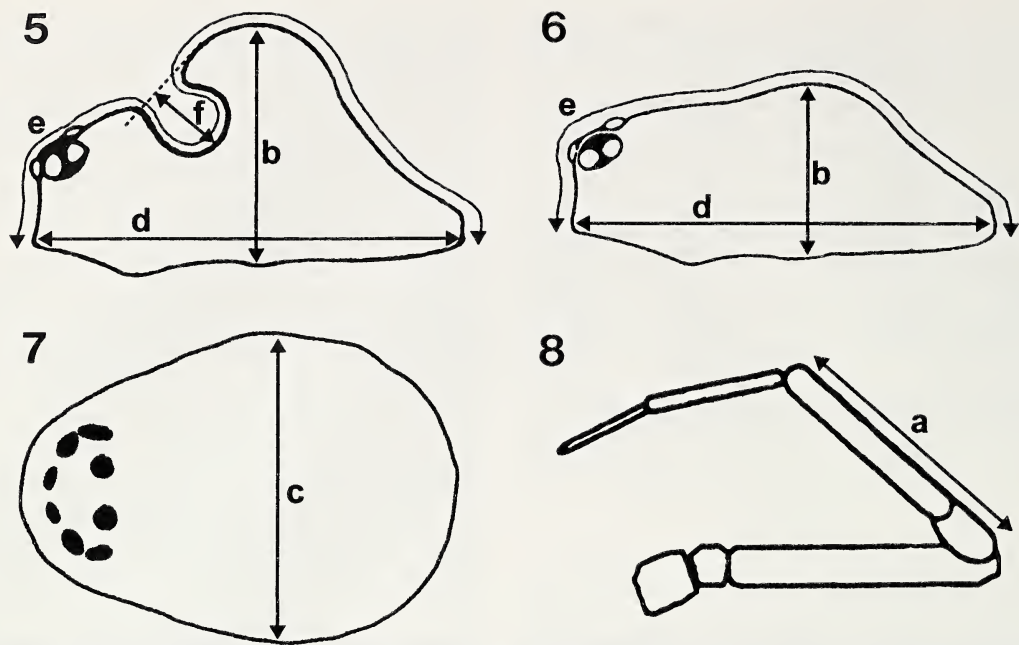
	PC1	PC2
Dorsal line along the prosoma	0.974	0.158
Prosomal notch	0.973	-0.025
Prosomal height	0.944	0.107
Prosomal width	0.317	0.751
Leg 1	0.001	0.802
Prosomal length	-0.341	0.863
Eigenvalues	2.89	1.99
Variance explained %	48.2	33.1

SD = 109) differs significantly from the one of the *tuberosus* morph (\bar{x} = 1443 μ m, SD = 71) (Mann-Whitney-*U*-Test, n_1 = 141, n_2 = 105, Z = 13.41, P < 0.001). The two morphs are significantly different in prosomal height, the prosoma of the *gibbosus* morph (\bar{x} = 551 μ m, SD = 41) being higher than the one of the *tuberosus* morph (\bar{x} = 425 μ m, SD = 43) (*t*-Test, t = -23.35, df = 244, P < 0.001).

Some males of the *tuberosus* morph showed a slight depression lacking hair on their prosoma. Comparison of depressions in the *tuberosus* morph (\bar{x} = 14 μ m, SD = 10) with the notches of the *gibbosus* morph (\bar{x} = 199 μ m, SD = 24) showed a significant difference (*U*-Test: n_1 = 114, n_2 = 105, Z = -12.781, P < 0.001). Furthermore, the prosoma of the *gibbosus* morph is significantly broader (\bar{x} = 810 μ m, SD = 34) as that of



Figures 1–4.—1. Lateral view of prosoma of the *gibbosus* form of *Oedothorax gibbosus*; 2. Dorsal view of the *gibbosus* form; 3. Lateral view of prosoma of the *tuberosus* form; 4. Dorsal view of the *tuberosus* form.



Figures 5–8.—Schematic representation of the characters measured. 5. Prosoma of *gibbosus* form, lateral view; 6. Lateral view of prosoma of the *tuberosus* form; 7. Dorsal view of prosoma of the *tuberosus* form; 8. First leg: a = length of patella plus tibia of the first leg, b = height of the prosoma, c = width of the prosoma, d = length of the prosoma, e = dorsal line along the prosoma, when viewed from the side, and f = depth of the notch.

the *tuberosus* morph (\bar{x} = 793 μ m, SD = 34) (t -Test: t = -3.68, df = 244, P < 0.001). The width of the prosoma significantly correlates with its height (Spearman rank correlation, r_s = 0.246, n = 246, P < 0.001).

Although the *gibbosus* morph has a broader and higher prosoma than the *tuberosus* morph

the difference in the length of the prosoma is only marginally significant (*gibbosus* morph: \bar{x} = 1007 μ m, SD = 31, *tuberosus* morph: \bar{x} = 1015 μ m, SD = 38; t -Test: t = 1.85, df = 244, P = 0.066). Interestingly, the two morphs do not differ in overall body size as measured by the leg character (*gibbosus* morph: \bar{x} = 861 μ m, SD = 32, *tuberosus* morph: \bar{x} = 865 μ m, SD = 32; t -Test: t = 1.078, df = 241, P = 0.285), although the leg measure significantly correlates with prosoma length (r_s = 0.5, n = 243, P < 0.001).

Relative numbers of the two morphs are highly skewed towards the *tuberosus* morph in all of the four locations examined (Table 2).

DISCUSSION

The results of this work show that the *gibbosus* form and the *tuberosus* form represent two distinct morphs of *O. gibbosus*, thus corroborating the rearing experiments by Mael-fait et al. (1990). We did not find any intermediate forms as supposed by Roberts (1987) although variation is considerable. This vari-

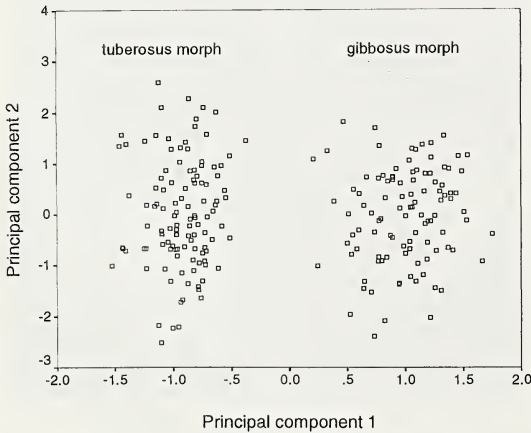


Figure 9.—Scatter plot of scores resulting from Principal Component Analysis.

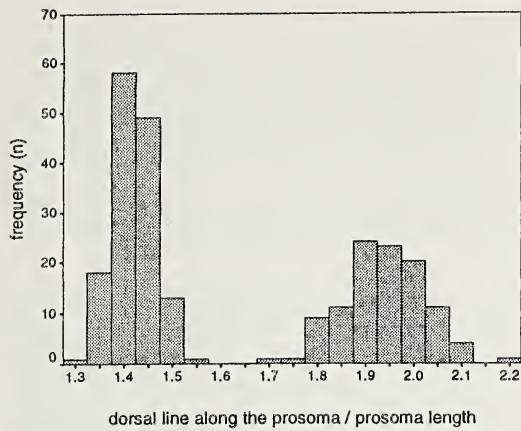


Figure 10.—Histogram of the indices of dorsal line of the prosoma and length of the first leg ($n = 246$).

ation led Roberts to assume intermediate states, when he discussed the existence of both morphs with regard to their assumed species status. Seen in the light of the work by Maelfait et al. (1990) and our data, the intermediates supposed by Roberts are within the variability of the morphs: a slight notch was apparent in extremes of *tuberosus* morph males which can nevertheless easily be assigned to one distinct morph or the other, as confirmed by Roberts (*in lit.* 1999). The two morphs are clearly characterized by the presence or absence of a deep hairy notch and a hump on the prosoma.

Our results are based on individuals caught in pitfall traps from various places in Belgium in different years. Variations between populations whose characteristics may differ in time and location are thus included. Investigating individuals of one population from one location in one year should result in even stronger morphometric distinction of the two morphs.

It is a surprising finding that the *gibbosus* morph occurs in lower numbers compared to the *tuberosus* morph in all four locations we investigated (Table 2). The data given by Maelfait et al. (1990), however, show higher relative numbers of the *gibbosus* morph in two of seven additional locations. Thus, altogether, the *tuberosus* morph is predominant in 9 of 11 locations, although the *gibbosus* morph is genetically dominant. Different collection methods as an explanation can be ruled out, as all specimens were collected by pitfall trap-

Table 2.—Numbers of *Oedothorax gibbosus* and *tuberosus* morphs collected by pitfall trapping at different localities in Belgium (collection de l'Institut Royal des Science Naturelles de Belgique, Bruxelles).

	<i>gibbosus tuberosus</i>		Rel. density
Moha (1977)	13	40	1:3.3
Moha (1979)	9	28	1:3.1
Virelles (1986)	9	16	1:1.8
Ethe (1981)	47	143	1:3.0
Antheit (1991)	18	52	1:2.9
Total	95	279	1:2.9

ping. Ecological factors seem to play an important role in determining the relative number of the two morphs. Examinations of the ecological demands and needs of both morphs may reveal a higher flexibility towards environmental changes of the *tuberosus* morph compensating for the genetic dominance of the *gibbosus* morph.

Sexual selection very likely also plays a role in balancing the dimorphism. Gustatorial courtship, the uptake of secretions by the female from a body part of the male during courtship is known for several linyphiid spiders (Lopez & Emerit 1981; Schaible et al. 1986; Schaible & Gack 1987). Indeed, SEM examinations of the notch revealed pores in the hair bases and ducts in the hairs of the *gibbosus* morph whereas no specializations were found in the prosoma of the *tuberosus* morph (Heinemann 1998). Preliminary investigation of courtship and mating behavior demonstrated that the chelicerae of the females contact the hairy notch of the *gibbosus* males (Heinemann 1998). If *gibbosus* males offer secretions to the female during courtship they should be sexually selected, i.e., females are expected to show preference for this morph.

Thus, we would expect the *gibbosus* morph to be sexually selected and the *tuberosus* morph to be naturally selected, possibly due to increased viability in comparison to *gibbosus* males. The role of gustatorial courtship, male mating behavior and female choice in combination with an investigation on ecological determinants need to be tackled to try to understand costs and benefits of the marked male dimorphism in *O. gibbosus*.

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MALE PALPAL BULBS AND HOMOLOGOUS FEATURES IN THERAPHOSINAE (ARANEAE, THERAPHOSIDAE)

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ABSTRACT. A first attempt to homologize male palpal bulb structures of theraphosine spiders is made, with the aim of providing systematic characters. The morphology and distribution of palpal bulb keels of over 60 species in 27 genera of Theraphosinae is presented and discussed. Four basic groups of keels were recognized and a terminology was created to name them: prolateral inferior and prolateral superior keels, for the two more or less parallel keels found on the prolateral bulb face; apical keel, for the ventral keel located just before the apex of the embolus; subapical keel, for a keel located just before the apical keel; and, retrolateral keel, for the keel located on the retrolateral region, originating on the apical region and extending backwards. Other palpal bulb keels, apart from these four basic groups, as well as other structures, were found in some genera and/or species, constituting apomorphies for these groups.

Keywords: Theraphosidae, male palpal bulbs, morphology of genitalia, systematics, homology

Theraphosidae is a speciose group of mygalomorph spiders with about 800 described species (Coddington & Levi 1991). This group presents enormous morphological homogeneity and many taxonomic problems (Raven 1990). The classification and identification is based mainly on structures such as stridulatory organs, fovea shape, small differences in the proportions between leg articles and other body parts, size and disposition of the eyes and scopulae, color patterns (Simon 1892; Pocock 1903; Mello-Leitão 1923; Schiapelli & Gerschman de Pikelin 1979; Raven 1985; Smith 1995, Prentice 1997), spermathecae shape (Schiapelli & Gerschman de Pikelin 1962) and urticating hair type (Cooke et al. 1972; Pérez-Miles et al. 1996). Many of these characters are conservative; and new species, based either on plesiomorphies or slight morphological variations, are still being described.

Palpal bulb characters, important for the classification and identification of spiders, have been not satisfactorily explored in Theraphosidae, as well as in other mygalomorph families. There is an extensive terminology for the parts of the complex copulatory organs of the entelegyne araneomorph spiders (Comstock 1910; Coddington 1990; Sierwald 1990) that is constantly used to characterize the taxa and provide characters for phylogenetic analysis (Coddington 1990; Sierwald 1990). In the

haplogyne mygalomorphs, the male bulb shape, as well as other genitalic characters, are commonly used in species identification, but rarely in identification of higher groups (Goloboff 1995). One reason is that much of the variation in these character complexes comes in the form of slight shape differences that are difficult to homologize across a large number of species (Goloboff 1995).

However, many authors agree that the shape of the palpal bulbs in Theraphosidae is constant and useful to characterize the taxa. For example, Pocock (1903) distinguished between species of *Pamphobeteus* Pocock 1901 using male bulb characters such as embolus width and keel shape. Other authors emphasized that species with similar male bulb shapes were probably very closely related. Valerio (1980a) called attention to the resemblance of the male bulb shape of some species of *Brachypelma* Simon 1891 with *Sericopelma* Ausserer 1875. At that time, these genera were considered to belong to different subfamilies (Grammostolinae and Theraphosinae) with which Valerio did not agree. Raven (1985) synonymized Grammostolinae with Theraphosinae; and, after the theraphosine genera revision of Pérez-Miles et al. (1996), it was demonstrated that they were two related genera, confirming Valerio's initial proposition. Bücherl (1957) also perceived that the male bulb shape could be useful in taxonomy

and stressed the relation between the similarity found in the male bulb shape and relationship. However, he thought of the male bulb shape as being only of "generic value," with which Schiapelli and Gerschman de Pikelin (1962) did not agree. These two authors consistently illustrated the male bulbs with high precision; and, in many cases, used their shape to separate species, as in the revision of *Acanthoscurria* Ausserer 1871 (Schiapelli & Gerschman de Pikelin 1964) and *Homoeomma* Ausserer 1871 (Gerschman de Pikelin & Schiapelli 1972).

Although the general resemblance of the palpal bulbs has been recognized as a relationship indicator, no attempt was made to homologize male bulb elements of theraphosid spiders. A first attempt is made here with species of Theraphosinae, a large New World subfamily with 36 genera and more than 300 described species that presents the male bulbs with a modified embolus, distally stout and broad or keeled (Raven 1985; Pérez-Miles et al. 1996). The aim of this paper is to homologize the theraphosine male bulb keels thus increasing the available number of characters for taxonomic work, particularly for cladistic analysis. Beside this, a terminology is proposed to name the homologous keels.

METHODS

The left male bulbs of 60 species belonging to 27 genera of Theraphosinae were analyzed and drawn with the aid of a stereomicroscope and a drawing tube. As the male bulb may rotate around its insertion in the palp, it was illustrated with the subtegulum pointing up, because the subtegulum, more constant in shape than the rest of the bulb, aids in positioning bulbs for comparison (Goloboff 1995). The classical homology criteria were used, i.e., (a) position criterion, (b) criterion of special, morphological similarity and (c) criterion of congruence with other characters (Remane 1956; Patterson 1982; Coddington 1990; Sierwald 1990). The last criterion is the most powerful way to test homology hypothesis, because it is the only test that discriminates useful comparisons from homoplasy (parallelism, convergence) and thus of value to the systematist (Patterson 1982).

Abbreviations.—*Institutions:* IBSP = Instituto Butantan, São Paulo; MCP = Museu de Ciência e Tecnologia da Pontifícia Univ-

ersidade Católica, Porto Alegre; MHNM = Museo Nacional de Historia Natural, Montevideo; MNRJ = Museu Nacional do Rio de Janeiro; MZSP = Museu de Zoologia da Universidade de São Paulo, São Paulo; RCW = Richard C. West private collection, Victoria. *Morphology:* A = apical keel; AEE = anterior embolus edge; DR = denticulate row; PA = paraembolic apophysis; PAC = *Acanthoscurria juruenicola* prolateral accessory keel; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SGA = subapical granular area of *Acanthoscurria ferina* and *A. insubtilis*; TA = tegular apophysis of *Homoeomma*; VC = ventral crest.

Species studied.—*Acanthoscurria atrox* Vellard 1924—IBSP 4247, Sacramento, Minas Gerais, Brazil; *A. chacoana* Brêthes 1909—IBSP 4727, Santo Antonio de Leverger, Mato Grosso, Brazil; *A. ferina* Simon 1892—IBSP 4742, Porto Velho, Rondônia, Brazil; *A. geniculata* (C.L. Koch 1842)—IBSP 7022, U.H.E. Tucuruí, Tucuruí, Pará, Brazil; *A. gomesiana* Mello-Leitão 1923—IBSP 4719, Itú, São Paulo, Brazil; *A. insubtilis* Simon 1892—IBSP 4713, Santo Antonio de Leverger, Mato Grosso, Brazil; *A. juruenicola* Mello-Leitão 1923—IBSP 4396, Alta Floresta, Mato Grosso, Brazil; *A. natalensis* Chamberlin 1917—IBSP 4204B, São Raimundo Nonato, Piauí, Brazil; *A. rondoniae* Mello-Leitão 1923—IBSP 2678, São Félix do Araguaia, Mato Grosso, Brazil; *A. sternalis* Pocock 1903—MNRJ, Jujuy, Argentina; *A. suina* Pocock 1903—MCP 2020, Vila Nova, Porto Alegre, Rio Grande do Sul, Brazil. *Aphonopelma seemani* (F.O. P.-Cambridge 1897)—IBSP 7019, Central América; *A. sp.*—IBSP 7047, Fresno County, California, U.S.A. *Brachypelma albopilosum* Valerio 1980—IBSP 7051, Guatemala; *B. boehmei* Schmidt & Klaas 1993—IBSP 7048, México; *B. emilia* (White 1856)—IBSP 7027, México; *B. klaasi* (Schmidt & Krause 1994)—IBSP 7050, México; *B. smithi* (F.O. P.-Cambridge 1897)—IBSP 4728, México. *Chromatopelma cyaneopubescens* (Strand 1907)—RCW, Punta Macolla, Panguana Península, Falcon State, Venezuela. *Crassiscrus lamanai* Reichling & West 1996—RCW, N. Belmopan (Western Highway), Belize. *Cyclosternum symmetricum* (Bücherl 1946)—IBSP 3367, Ilha Bela, São Paulo, Brazil. *Cyriocosmus cf. elegans* (Simon 1889)—IBSP 4948, U.H.E. Balbina, Presidente Figueiredo, Amazonas, Brazil; *C. cf. sellatus* (Simon 1889)—IBSP 4947, U.H.E. Samuel, Porto Velho, Rondônia, Brazil. *Cyrtopholis portoricae* Chamberlin 1917—RCW, NW Guayama, Porto Rico; *C. palmarum* Schiapelli & Gerschman 1945—IBSP 4730, Paranaíba, Mato Grosso, Brazil. *Euathlus truculentus*

Table 1.—Homologous keels present, weakly developed (+), developed (++), well developed (+++), or absent (–) in representative taxa of Theraphosinae. A = apical; AEE = anterior embolus edge; DR = denticulate row; EPF = embolus prolateral face; PA = paraembolic apophysis; PI = prolateral inferior; PS = prolateral superior; R = retrolateral; SA = subapical; SGA = subapical granular area; TA = tegular apophysis; VC = ventral crest; cx = embolus prolateral face straight or convex; ec = embolus prolateral face extremely concave; sc = embolus prolateral face slightly concave above and under the prolateral keel.

	PS	PI	A	SA	R	EPF	Other structures
<i>Euathlus truculentus</i>	–	–	–	–	–	cx	VC
<i>Cyriocosmus</i> cf. <i>elegans</i>	+	–	–	–	–	cx	short PA
<i>Cyriocosmus</i> cf. <i>sellatus</i>	?	–	–	–	–	cx	long PA
<i>Grammostola rosea</i>	++	++	–	–	–	cx	none
<i>Grammostola acteon</i>	++	++	–	–	–	cx	none
<i>Grammostola iheringi</i>	++	++	–	–	–	cx	none
<i>Grammostola longimana</i>	++	++	–	–	–	cx	none
<i>Grammostola pulchra</i>	++	++	–	–	–	cx	none
<i>Plesiopelma insulare</i>	++	++	–	–	–	cx	none
<i>Homoeomma montanum</i>	++	++	–	–	–	cx	TA
<i>Homoeomma stradlingi</i>	++	++	–	–	–	cx	TA
<i>Tmesiphantes nubilus</i>	++	++	–	–	–	cx	none
<i>Phrixotrichus scrofa</i>	++	++	–	–	–	cx	none
<i>Hapalopus</i> sp.	+	+++	–	–	–	cx	PI split in two
<i>Cyclosternum symmetricum</i>	++	++	–	–	–	cx	none
<i>Chromatopelma cyaneopubescens</i>	++	+++	++	–	–	cx	crested triangular PI
<i>Metriopelma</i> sp.	++	+++	++	–	?	cx	two R keels ?; crested triangular PI
<i>Aphonopelma seemani</i>	+	++	++	–	–	cx	PI with a DR
<i>Aphonopelma</i> sp.	–	++	+	–	–	cx	none
<i>Sphaerobothria hoffmani</i>	+	++	++	–	–	cx	PI with a DR
<i>Acanthoscurria atrox</i>	+++	+++	+	–	–	cx	none
<i>Acanthoscurria chacoana</i>	+++	+++	+	–	–	cx	none
<i>Acanthoscurria ferina</i>	+	+	+++	?	–	cx	SGA
<i>Acanthoscurria geniculata</i>	+++	+++	+	–	–	cx	none
<i>Acanthoscurria gomesiana</i>	+++	+++	–	–	–	cx	none
<i>Acanthoscurria insubtilis</i>	++	++	+++	?	–	cx	SGA
<i>Acanthoscurria juruenicola</i>	+++	+++	+	–	–	cx	prolateral accessory keel
<i>Acanthoscurria natalensis</i>	+	++	+	–	–	cx	none
<i>Acanthoscurria rondoniae</i>	+	++	+	–	–	cx	none
<i>Acanthoscurria sternalis</i>	++	++	++	DR	–	cx	none
<i>Acanthoscurria suina</i>	+++	+++	–	–	–	cx	none
<i>Phormictopus cancerides</i>	++	++	++	DR	–	cx	none
<i>Phormictopus cubensis</i>	++	++	++	DR	–	cx	none
<i>Cyrtopholis portoricae</i>	+	+	–	–	–	cx	none
<i>Cyrtopholis palmarum</i>	++	++	++	–	–	cx	none
<i>Eupalaestrus campestratus</i>	++	++	++	DR	++	sc	none
<i>Eupalaestrus weijenberghi</i>	++	++	++	DR	++	sc	none
<i>Eupalaestrus anomalus</i>	++	++	++	++	++	sc	none
<i>Lasiadora klugi</i>	++	++	++	++	++	sc	none
<i>Lasiadora mariannae</i>	++	++	++	++	++	sc	none
<i>Lasiadora subcanens</i>	++	++	++	++	++	sc	none
<i>Nhandu carapoensis</i>	++	++	++	++	++	sc	none
<i>Vitalius sorocabae</i>	++	++	++	++	++	sc	none
<i>Vitalius platyomma</i>	++	++	++	++	++	sc	none
<i>Vitalius roseus</i>	++	++	++	+	++	sc	none
<i>Vitalius cesteri</i>	++	++	++	++	++	sc	none

Table 1.—Continued.

	PS	PI	A	SA	R	EPF	Other structures
<i>Vitalius tetracanthus</i>	++	++	++	++	++	sc	none
<i>Crassicrus lamanai</i>	++	++	++	—	++	sc	double A, one of them denticulate?
<i>Pamphobeteus</i> cf. <i>nigricolor</i>	++	+	+++	—	++	ec	long R
<i>Pamphobeteus</i> cf. <i>ornatus</i>	++	—	+++	—	++	ec	R half of the embolus long
<i>Pamphobeteus</i> sp.	++	—	+++	—	++	ec	R a third of the embolus long
<i>Xenesthis immanis</i>	++	++	+++	—	++	ec	none
<i>Brachypelma albopilosum</i>	++	++	+++	—	—	ec	none
<i>Brachypelma boehemei</i>	++	+	+++	—	—	ec	none
<i>Brachypelma emilia</i>	++	—	+++	—	—	ec	none
<i>Brachypelma klaasi</i>	++	—	+++	—	—	ec	AEE sinuous
<i>Brachypelma smithi</i>	++	+	+++	—	—	ec	none
<i>Megaphobema</i> sp.	++	++	+++	—	—	ec	prolateral accessory keels
<i>Theraphosa blondi</i>	++	—	+++	—	—	ec	AEE keels fused
<i>Pseudotheraphosa apophysis</i>	++	—	+++	—	—	ec	AEE keels fused

Ausserer 1875—IBSP 3744, Valparaíso, Chile. *Eupalaestrus campestratus* (Simon 1891)—IBSP 4149, Coxim, Mato Grosso do Sul, Brazil; *E. weijenberghi* (Thorell 1894)—MHNM, Montevideo, Uruguay; *E. anomalus* (Mello-Leitão 1923)—IBSP 4747, Alta Floresta, Mato Grosso, Brazil. *Grammostola rosea* (Walckenaer 1837)—IBSP 7067, Chile; *G. acteon* (Pocock 1903)—IBSP 3876, Mallet, Paraná, Brazil; *G. iheringii* (Keyserling 1891)—IBSP 4498, Blumenau, Santa Catarina, Brazil; *G. longimana* Mello-Leitão 1921—IBSP 3754, Moreira, Paraná, Brazil; *G. pulchra* Mello-Leitão 1921—IBSP 3519, Brazil. *Hapalopus* sp.—IBSP 7046, U.H.E. Tucuruí, Tucuruí, Pará, Brazil. *Homoeomma montanum* (Mello-Leitão 1923)—IBSP 7045, Paranaipiacaba, São Paulo, Brazil; *H. stradlingi* O. P. Cambridge 1881—IBSP 4683, Teresópolis, Rio de Janeiro, Brazil. *Lasiodora klugi* (C.L. Koch 1841)—IBSP 7013, Caruarú, Pernambuco, Brazil; *L. mariannae* Mello-Leitão 1921—IBSP 2525, Ouro Preto, Minas Gerais, Brazil; *L. subcanens* Mello-Leitão 1921—IBSP 6380, Iconha, Espírito Santo, Brazil. *Megaphobema* sp.—MNRJ 14002, Rio Purús, Brazil. *Metriopelma zeburata* Banks 1909—IBSP 7069, Central América. *Nhandu carapoensis* Lucas 1981—IBSP 6555, Piraputanga, Mato Grosso do Sul, Brazil. *Pamphobeteus* cf. *nigricolor* (Ausserer 1875)—IBSP 7024, Medellín, Colombia; *Pamphobeteus* cf. *ornatus* Pocock 1903—IBSP 7070, no locality; *Pamphobeteus* sp.—IBSP 4944, U.H.E. Samuel, Porto Velho, Rondônia, Brazil. *Phormictopus cancerides* (Latreille

1806)—RWC, Barahona, Dominican Republic; *P. cubensis* Chamberlin, 1917—MNRJ 13264, Cuba. *Phrixotrichus scrofa* (Molina 1788)—IBSP 3805, Chile. *Plesiopelma insulare* (Mello-Leitão 1923)—IBSP 4493, Tapiraí, São Paulo, Brazil. *Pseudotheraphosa apophysis* Tinter 1991—IBSP 7049, Brazil/Venezuela boundary. *Sphaerobothria hoffmani* Karsch 1879—RCW, Moraña, San Jose, Costa Rica. *Theraphosa blondi* (Latreille 1804)—IBSP 7029, U.H.E. Tucuruí, Tucuruí, Pará, Brazil. *Tmesiphantes nubilus* Simon 1892—IBSP 7068, Rio de Contas, Bahia, Brazil. *Vitalius sorocabae* (Mello-Leitão 1923)—IBSP 5073, Ibiúna, São Paulo, Brazil; *V. platyomma* (Mello-Leitão 1923)—IBSP 4812, São Sebastião, São Paulo, Brazil; *V. roseus* (Mello-Leitão 1923)—IBSP 6314, Assis, São Paulo, Brazil; *V. cesteri* (Mello-Leitão 1923)—IBSP 6585, Juquitiba, São Paulo, Brazil; *V. tetracanthus* (Mello-Leitão 1923)—IBSP 3203, Americana, São Paulo, Brazil. *Xenesthis immanis* (Ausserer 1875)—IBSP 7026, Venezuela.

RESULTS AND DISCUSSION

Theraphosine male bulb general morphology.—The theraphosine male bulb is pyriform and presents a distally stout and broad or keeled embolus and a large subtegulum, extending down the bulb for half the length of tegulum (Raven 1985). The presence of keels is considered one of the three synapomorphies

of Theraphosinae (Raven 1985; Pérez-Miles et al. 1996). Some groups present conspicuous and exclusive structures such as the paraembolic apophysis (PA) in *Cyriocosmus* Simon 1903 species (Figs. 17, 18) (Raven 1985; Pérez-Miles et al. 1996) or a digitiform tegular apophysis (TA) in *Homoeomma* species (Figs. 13, 14) (Gerschman de Pikelin & Schiapelli 1972; Pérez-Miles et al. 1996). In many species, the embolus is distally flattened, giving them a concave/convex, spoon-like appearance (Figs. 5, 6, 43, 44). I found this occurred to different degrees, from an almost circular to an extreme concave-retrolateral/convex-prolateral embolus shape (Figs. 1–6). Figs. 1, 2 show an almost circular embolus in which the retrolateral side is straight or slightly convex. The genera *Grammostola* Simon 1892, *Euathlus* Ausserer 1875, *Plesiopelma* Pocock 1901, *Homoeomma*, *Cyriocosmus*, *Tmesiphantes* Simon 1892, *Phrixotrichus* Simon 1892, *Hapalopus* Ausserer 1875, *Cyclosternum* Ausserer 1871, *Chromatopelma* Schmidt 1995, *Metriopelma* Becker 1878, *Aphonopelma* Pocock 1901, *Sphaerobothria* Karsch 1879, *Cyrtopholis* Simon 1892, *Phormictopus* Pocock 1901, and *Acanthoscurria* are included in this group. Other genera, such as *Crassiscrus* Reichling & West 1996, *Eupa-laestrus* Pocock 1901, *Lasiadora* C.L. Koch 1850, *Vitalius* Lucas, Silva Júnior & Bertani 1993, and *Nhandu* Lucas 1981 (Figs. 3, 4) have the embolus slightly distally concave in the areas above and under the retrolateral keel (see the next item for the keel terminology). In the genera *Pamphobeteus* Pocock 1901, *Xenesthis* Simon 1891, *Megaphobema* Pocock 1901, *Brachypelma*, *Pseudothephosa* Tinter 1991, and *Theraphosa* Thorell 1870 these areas are extremely concave, giving them the characteristic spoon-like appearance (Figs. 5, 6).

Theraphosine male bulb keels and homology.—The results of a comparative study carried out on the male bulb keels of 60 species of Theraphosinae is summarized in Figs. 1–44 and Table 1. Four main groups of homologous keels can be recognized and are described.

Prolateral keels: Comprises two parallel keels, superior (PS) and inferior (PI), present in the prolateral area of the embolus. These keels follow the twisted embolus shape of many species. The homology of the prolateral

keels is evident in many genera. *Grammostola* (Figs. 9, 10), *Plesiopelma* (Figs. 11, 12), *Homoeomma* (Figs. 13, 14), *Tmesiphantes*, and *Phrixotrichus* have a tapering and twisted embolus with only the prolateral keels present, posing no difficulties in establishing the homology between them. The differences in these palpal bulbs concern the extension of the keels, the distance between them and their size.

In some taxa with a slender and more or less straight embolus, the prolateral keels are not so evident. That is what occurs in some species of *Cyrtopholis* and *Aphonopelma* (Figs. 19, 22). In *Aphonopelma* these keels are weakly developed and are confined to the distal tip of the embolus, and sometimes only one keel is visible (Figs. 21, 22). However, in other species, such as *A. seemani* (Figs. 19, 20), the two keels are evident, though the upper one is not well-developed. The *Aphonopelma seemani* and *Sphaerobothria hoffmani* bulbs are very similar, as pointed out by Valerio (1980b) (Figs. 19, 20, 23, 24). I found that the two species share a reduced PS and the well-developed PI keel, presenting a denticulate row backwards from its middle, that could constitute a synapomorphy of *Aphonopelma* + *Sphaerobothria*. This view differs from that of the cladogram from Pérez-Miles et al. 1996 (Fig. 45) and is discussed under “conclusions.” Other *Aphonopelma* species also possess this denticulate row, as can be seen in Pickard-Cambridge (1897), plate I, fig. 16, for *Aphonopelma serratum* (Simon 1890) and Smith (1995), fig. 261, for *Aphonopelma crinitum* (Pocock 1901). The absence of both the PS and the PI denticles could be seen as apomorphies to the group of *Aphonopelma* species found in the northernmost distribution of the genus (Smith 1995).

In some genera with short, stout and non spoon-like embolus, such as many species of *Acanthoscurria* (Figs. 25–30), *Hapalopus* (Figs. 15, 16), *Metriopelma*, and *Chromatopelma*, one or both of the prolateral keels are well-developed. In some *Acanthoscurria* species such as *A. atrox* (Figs. 25, 26), *A. geniculata* and *A. juruenicola* (Figs. 29, 30), these keels are so well-developed and twisted that the general shape of the organ is odd; and at first sight, it is difficult to recognize these keels as homologous to the anterior ones. The PS is very raised on its most proximal portion;

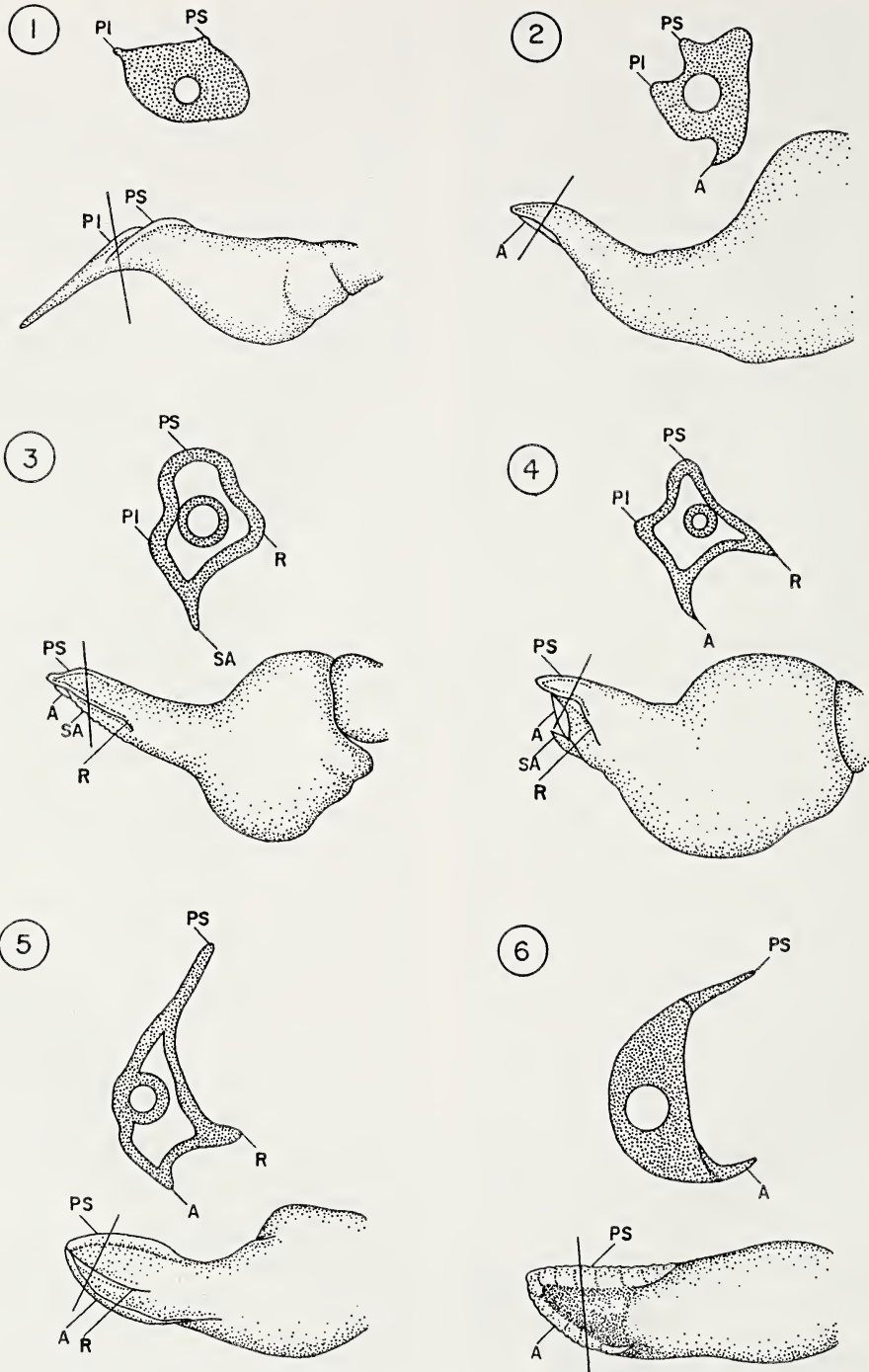
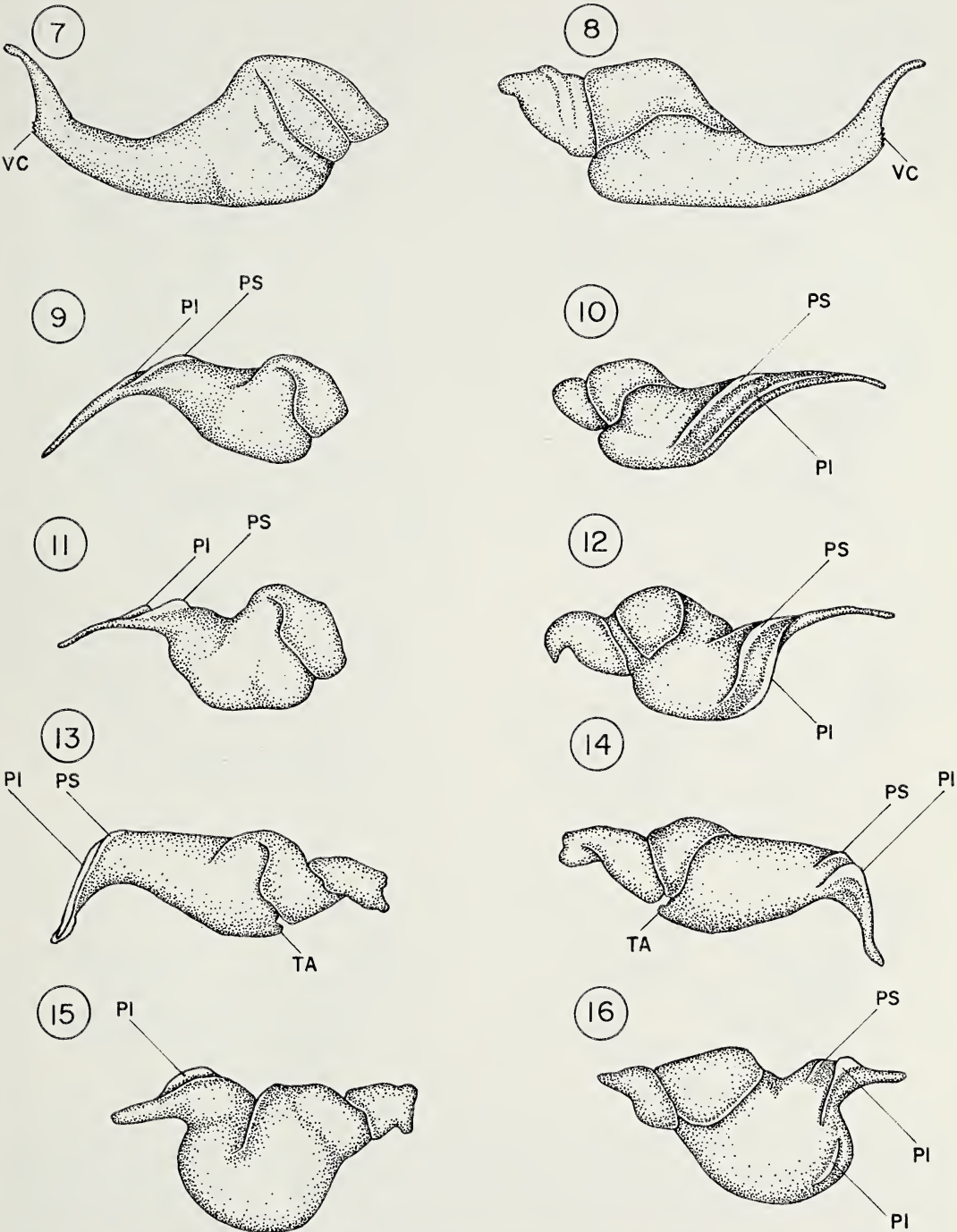
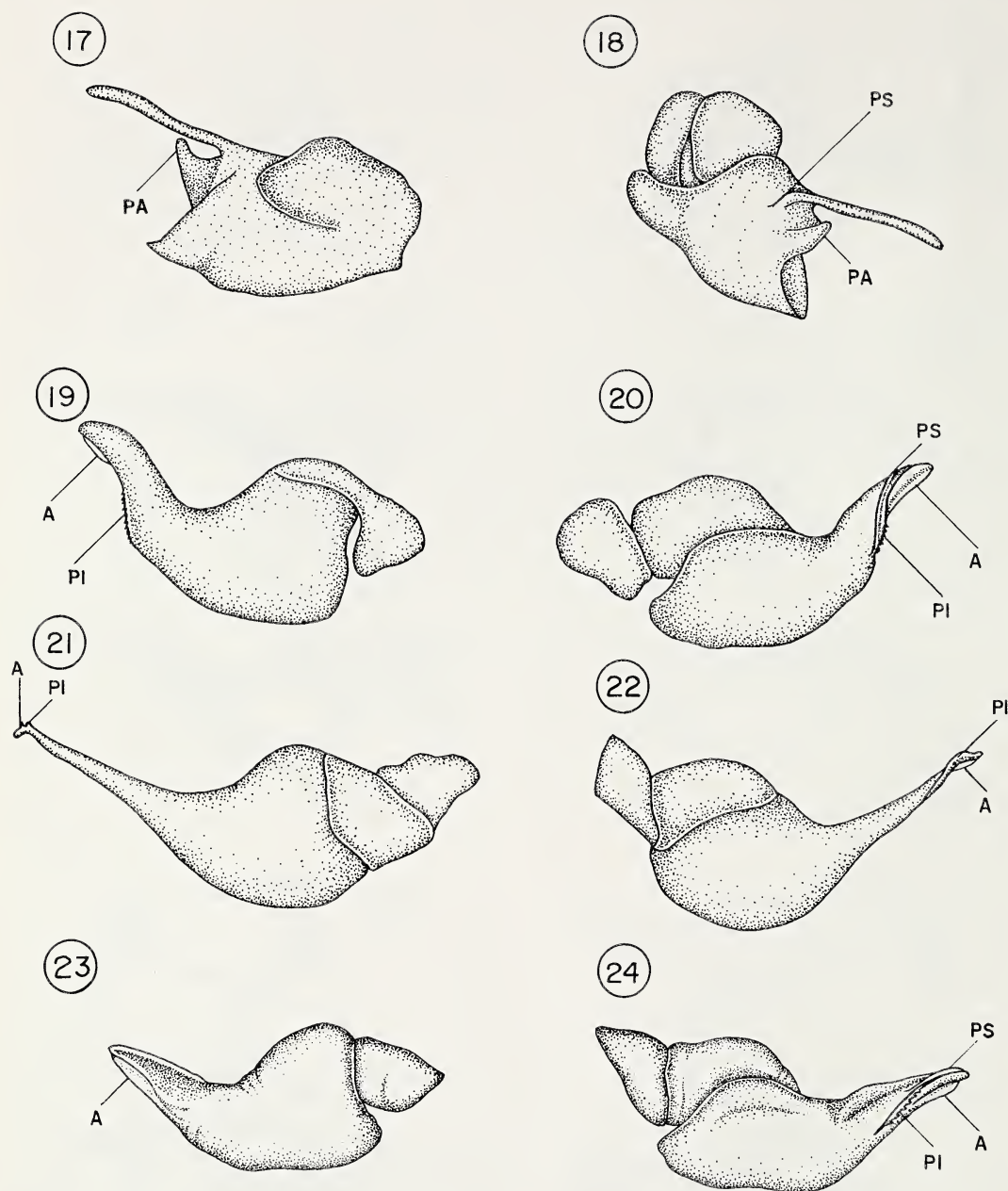


Figure 1-6.—Transverse view of the left embolus of some representative theraphosine species. 1, *Grammostola aceton* (Pocock 1903); 2, *Aphonopelma seemani* (F.O. P. -Cambridge 1897); 3, *Eupalaestrus campestratus* (Simon 1891); 4, *Vitalius tetracanthus* (Mello-Leitão 1923); 5, *Pamphobeteus* sp.; *Theraphosa blondi* (Latreille 1804). Abbreviations: A = apical keel; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SA = subapical keel.



Figures 7–16.—Left male bulbs of some representative theraphosine species. 7, 8. *Euathlus truculentus* Ausserer 1875. 7, Retrolateral view; 8, Prolateral view. 9, 10. *Grammostola acteon* (Pocock 1903). 9, Retrolateral view; 10, Prolateral view; 11, 12. *Plesiopelma insulare* (Mello-Leitão 1923). 11, Retrolateral view; 12, Prolateral view; 13, 14. *Homoeomma montanum* (Mello-Leitão 1923). 13, Retrolateral view; 14, Prolateral view; 15, 16. *Hapalopus* sp. 15, Retrolateral view; 16, Prolateral view. Abbreviations: PI = prolateral inferior keel; PS = prolateral superior keel; TA = tegular apophysis; VC = ventral crest.



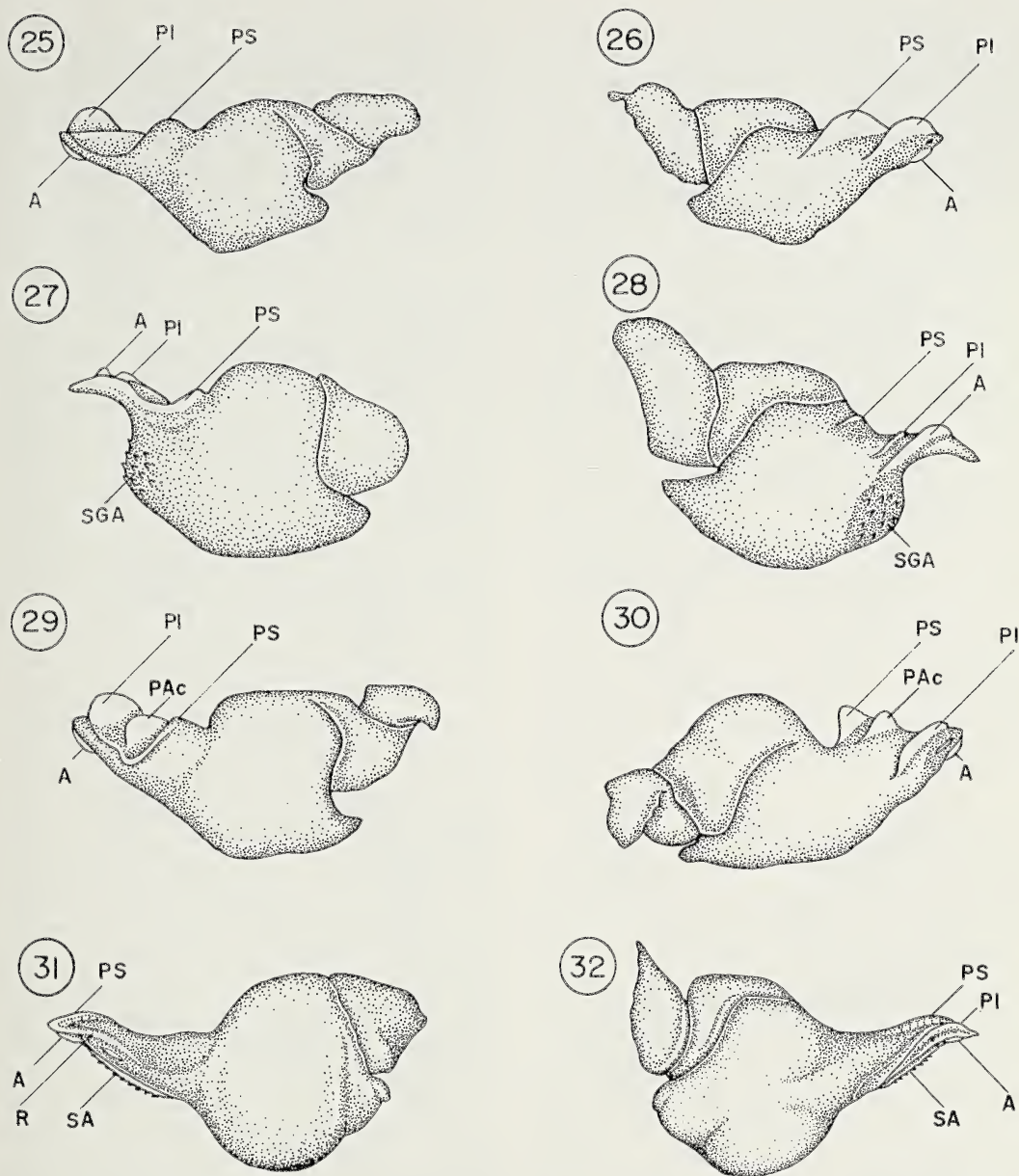
Figures 17-24.—Left male bulbs of some representative theraphosine species (continued). 17, 18. *Cyriocosmus* cf. *elegans* (Simon 1889). 17, Retrolateral view; 18, Prolateral view; 19, 20. *Aphonopelma seemani* (F.O. P.-Cambridge 1897). 19, Retrolateral view; 20, Prolateral view. 21, 22. *Aphonopelma* sp. 21, Retrolateral view; 22, Prolateral view; 23, 24. *Sphaerobothria hoffmani* Karsch 1879. 23, Retrolateral view; 24, Prolateral view. *Abbreviations:* A = apical keel; PA = paraembolic apophysis; PI = prolateral inferior keel; PS = prolateral superior keel.

and towards the apex it becomes lower, constituting the upper bulb edge.

The genera *Hapalopus*, *Metriopelma*, and *Chromatopelma* have the PI very well-developed, and in *Hapalopus* it is split in two (Figs.

15, 16). The genera *Metriopelma* and *Chromatopelma* have the PI presenting a triangular shape, with no such division.

In another group that includes *Eupalaestrus* (Figs. 31, 32), *Vitalius* (Figs. 33, 34), *Lasio-*

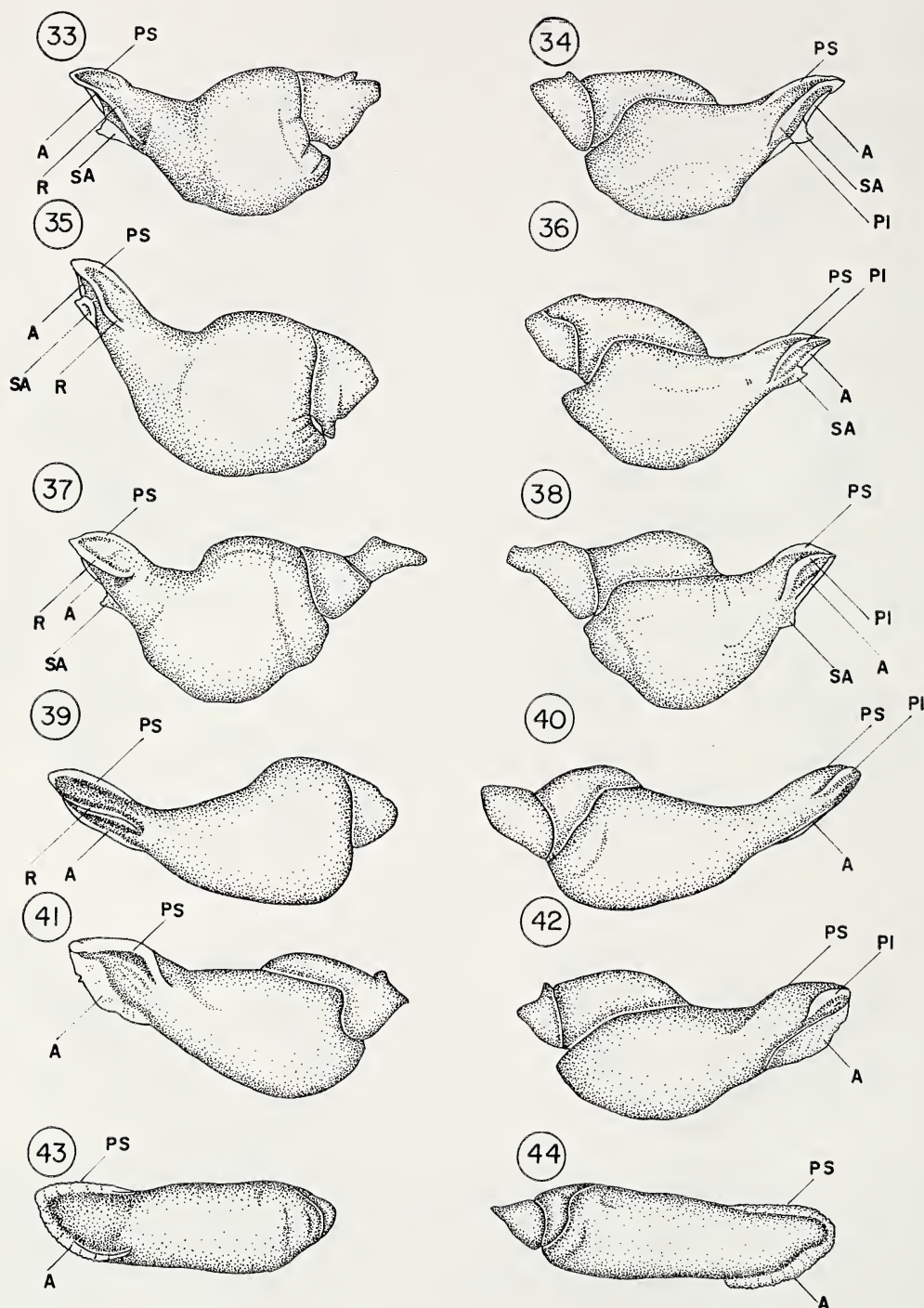


Figures 25-32.—Left male bulbs of some representative theraphosine species (continued). 25, 26. *Acanthoscurria atrox* Vellard 1924. 25, Retrolateral view; 26, Prolateral view. 27, 28. *Acanthoscurria insubtilis* Simon 1892. 27, Retrolateral view; 28, Prolateral view. 29, 30. *Acanthoscurria juruenicola* Mello-Leitão 1923. 29, Retrolateral view; 30, Prolateral view. 31, 32. *Eupalaestrus campestratus* (Simon 1891). 31, Retrolateral view; 32, Prolateral view. *Abbreviations:* A = apical keel; PAc = prolateral accessory keel; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SA = subapical keel; SGA = subapical granular area.

dora (Figs. 35, 36) and *Nhandu* (Figs. 37, 38), the prolateral keels are confined to the distal part of the embolus and, as observed in some *Acanthoscurria* species, the PS forms the upper edge of the distal embolus. These keels

are rounded in this group, differing from sharp keels present in other genera.

In the group with a spoon-like embolus (*Pamphobeteus* (Figs. 39, 40), *Xenesthis*, *Megaphobema*, *Brachypelma* (Figs. 41, 42),



Figures 33-44.—Left male bulbs of some representative theraphosine species (continued). 33, 34. *Vitalius sorocabae* (Mello-Leitão 1923). 33, Retrolateral view; 34, Prolateral view. 35, 36. *Lasiodora klugi* (C.L. Koch 1841). 35, Retrolateral view; 36, Prolateral view; 37, 38. *Nhandu carapoensis* Lucas 1981. 37, Retrolateral view; 38, Prolateral view; 39, 40. *Pamphobeteus* cf. *nigricolor* (Ausserer 1875). 39, Retrolateral view; 40, Prolateral view. 41, 42. *Brachypelma boehmei* Schmidt & Klaas 1993. 41, Retrolateral view; 42, Prolateral view. 43, 44. *Theraphosa blondi* (Latreille 1804). 43, Retrolateral view; 44, Prolateral view. Abbreviations: A = apical keel; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SA = subapical keel.

Theraphosa (Figs. 43, 44), and *Pseudotheraphosa*) the PS also constitutes the upper edge of the embolus, but it is thinner and retrolaterally directed. The PI is weakly developed or absent in some species of the genera *Pamphobeteus* (Figs. 39, 40), *Xenesthis*, *Megaphobema*, and *Brachypelma* (Figs. 41, 42). In *Theraphosa* (Figs. 43, 44) and *Pseudotheraphosa* there is no vestige of the PI.

Apical keel (A): A small, slightly transparent keel located just below the apex of the embolus. It is highly developed in some groups and usually presents a fissure delimiting its area. The apical keel is absent in the genera *Grammostola*, *Euathlus*, *Cyriocosmus*, *Plesiopelma*, *Homoeomma*, *Tmesiphantes*, *Phrixotrichus*, *Hapalopus* and *Cyclosternum*. In the genus *Acanthoscurria* (Figs. 25, 26, 29, 30) and *Aphonopelma* (Figs. 19–22) it is very small in some species and seems to be absent in others (see Table 1). In the genera *Eupalaestrus* (Figs. 31, 32), *Vitalius* (Figs. 33, 34), *Lasiodora* (Figs. 35, 36), and *Nhandu* (Figs. 37, 38) it is always present, but it is small and confined to the distal part of the embolus. In the group with spoon-like embolus, however, it has a great backward development, extending for almost all the inferior embolus edge. Thus, the two keels on the edges of these characteristic male bulbs derived independently. The superior keel is derived from the PS and the lower keel from the A. In the male bulbs of *Pamphobeteus* (Figs. 39, 40), *Xenesthis*, *Brachypelma* (Figs. 41, 42) and *Megaphobema* species, these two keels are not anteriorly fused and are positioned at different levels. In *Theraphosa* (Figs. 6, 43, 44) and *Pseudotheraphosa* the PS and the A keels are anteriorly completely fused, constituting a unique piece surrounding the entire embolus edge. It is possible to recognize this as being the result of such a fusion only through the comparison with species of the other genera previously cited that do not have this fusion but have a very similar spoon-like embolus. Furthermore, in many species, as in *Brachypelma boehmei* (Figs. 41, 42) there is a fissure which delimits the apical keel boundary from the remaining part of the embolus. This does not occur with the PS, where no delimitation is visible, suggesting they had distinct origins.

Subapical keel (SA): A keel located just below the apical keel. It assumes a triangular

shape in the genera *Vitalius* (Figs. 33, 34), *Lasiodora* (Figs. 35, 36), and *Nhandu* (Figs. 37, 38). In *Eupalaestrus campestratus* (Figs. 31, 32), *E. weijenberghi*, *Phormictopus*, and *A. sternalis* it is constituted by a denticulate row (DR) which is a primary homologue to the triangular keel present in the other genera above.

Retrolateral keel (R): A keel developed retrolaterally from the apex of the embolus to the rear. This keel is shared by species of *Crassiscrus*, *Eupalaestrus* (Figs. 31, 32), *Vitalius* (Figs. 33, 34), *Lasiodora* (Figs. 35, 36), *Nhandu* (Figs. 37, 38), *Pamphobeteus* (Figs. 39, 40), and *Xenesthis*. It seems to be lost in the genera *Brachypelma* (Figs. 41, 42), *Megaphobema*, *Theraphosa* (Figs. 43, 44), and *Pseudotheraphosa*, constituting possibly a synapomorphy (Fig. 45). This option seems to be more parsimonious, because the genera *Pamphobeteus* and *Xenesthis* share other characters with these genera, such as the spermathecae shape, the spoon-like embolus and the well-developed apical keel. Additional steps are required if they are considered as independently acquired, whereas if the absence of the R is considered a reversal, only one step is required.

Other keel groups: Apart from these four basic groups of keels, there are others not so widespread and such are sometimes confined to only one species. An example is a small keel found between the prolateral keels in *Acanthoscurria juruenicola* (PAC, Figs. 29, 30). The general shape of the male bulb is the same as the related species *A. atrox* (Figs. 25, 26) and *A. gomesiana* due to the well-developed PS and PI, but only *A. juruenicola* and perhaps *A. geniculata* have this keel, which is smaller and isolated from the PS and PI. Thus, this structure is called "*Acanthoscurria juruenicola* prolateral accessory keel (PAC)," following Coddington 1990, as a way of avoiding confusion with the terminology among other similar but non-homologous keels.

In a similar way, the *Megaphobema* species examined has, in the prolateral area, some keels other than the prolateral keels, and, if they are present in the other species of *Megaphobema*, they are called "*Megaphobema* prolateral accessory keels." Also, in the species *Acanthoscurria ferina* and *Acanthoscurria insubtilis* there is a granular area in the

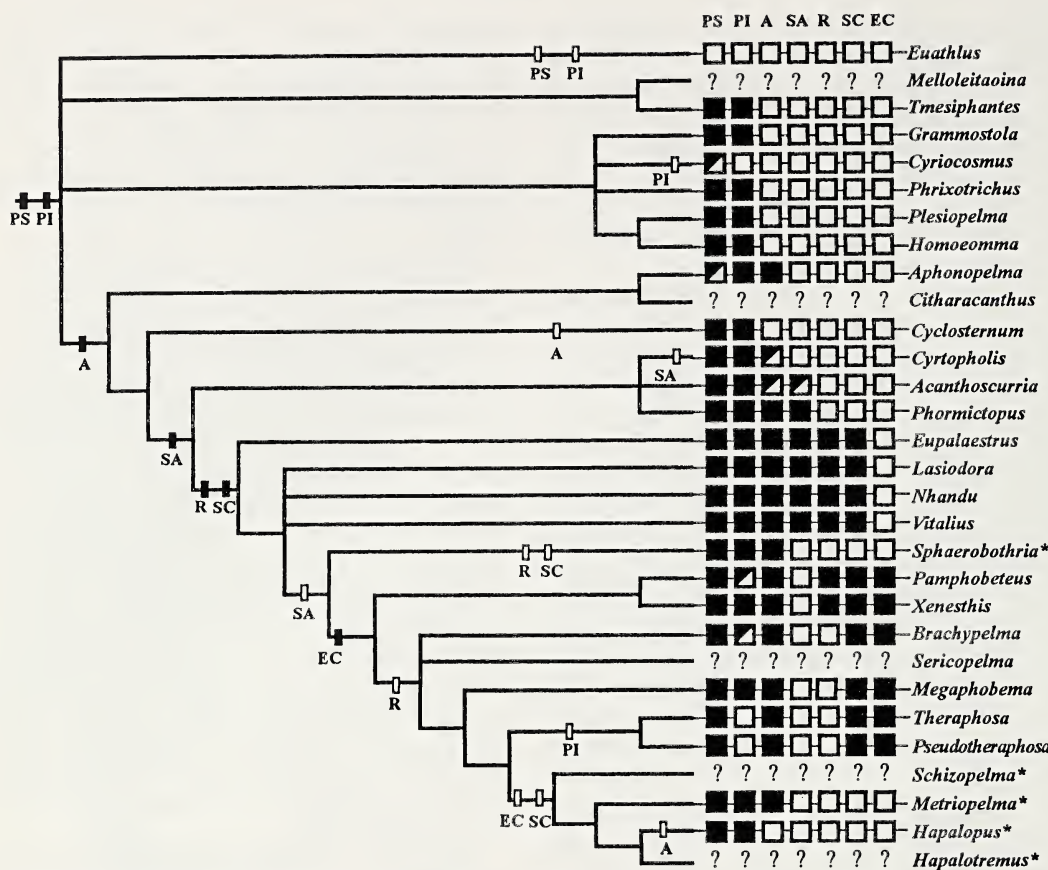


Figure 45.—Probable evolution of male palpal bulb keels in Theraphosinae. Bulb characters were mapped on the cladogram of Pérez-Miles et al. (1996). Taxa which show incongruence between the character evolution proposed here and in the cladogram of Pérez-Miles et al. (1996) are indicated by an asterisk. See text for further discussions. *Abbreviations:* ? = information absent, refers to genera which did not have specimens examined in this work. A = apical keel; EC = embolus prolateral face extremely concave; PI = prolateral inferior keel; PS = prolateral superior keel; R = retrolateral keel; SA = subapical keel; SC = embolus prolateral face slightly concave above and under the prolateral keel. SC and EC were treated as additive multistate characters. Black rectangle = synapomorphy; white rectangle = reversal. Black square = present; white square = absent; upper black triangle in a square = character exhibiting interspecific variation.

ventral subapical region (SGA) that seems to be a synapomorphy of these species and is called *Acanthoscurria ferina* and *A. insubtilis* subapical granular area.

The opposite occurs in some species of the genera *Cyriocosmus* and *Euathlus*, where the four basic groups of keels are absent. The palpal bulb of *Cyriocosmus* (Figs. 17, 18) is highly modified and the species possess from short to large paraembolic apophysis (PA) (see Schiapelli & Gerschman de Pikelin 1973). In some species studied I have found some vestiges of the superior prolateral keel and I believe that, with an increased knowl-

edge of the genus, there is the possibility that some basal species with a less modified embolus can be found, which still retain these keels plesiomorphically.

In *Euathlus truculentus*, however, the only keel present is one ventral medial crest (VC, Figs. 7, 8) not found in other theraphosine species. There is no vestige of the prolateral keels that, as shown above, are the most plesiomorphic ones in Theraphosinae. Because of the basal position in a politomy occupied by *Euathlus* in the cladistic analysis of Theraphosinae by Pérez-Miles et al. (1996) (Fig. 45), there are two possibilities: (1). The pro-

lateral keels are a synapomorphy of all theraphosine except *Euathlus*; in this case *Euathlus* is the most basal taxon of all Theraphosinae. (2). The prolateral keels were lost in *Euathlus truculentus*. The two possibilities seem equally parsimonious.

CONCLUSIONS

As shown above, the theraphosine palpal bulbs present some basic groups of keels which are widespread among almost all theraphosine species. These five keels were homologized through the classical criteria of homology, i.e., they presented the same relative position in the bulbs; they presented morphological similarity, considering that no extreme and improbable changes were seen; and they were in accordance with the other characters, in this case the other keels. The last one is the most powerful test of homology and the most important to systematics (Patterson 1982). Also, the co-occurrence of the five proposed keels in some species is in accordance with the conjunction test of Patterson (1982), i.e., they constitute five homologous keels. Keels other than these basic ones were found and some morphological modifications were seen. I consider this only one more argument to justify that these structures, overlooked for so long, could be valuable for taxonomy and systematic work due to their great morphological interspecific variability. Of course, this work must be seen as an initial approach and surely many alterations will take place when more information on theraphosine morphology and hypothesis of relationship become available, a reason why no phylogenetic analysis was carried out here. However, when considering the cladogram of theraphosine genera proposed by Pérez-Miles et al. 1996, I found concordance with the keels evolution proposed here, with two exceptions (Fig. 45). The first one is the genus *Sphaerobothria* which, as discussed earlier, has a very similar bulb when compared with some *Aphonopelma* species. The second is the branch including *Schizopelma*, *Metriopelma*, *Hapalopus*, and *Hapalotremus*. The position of these branches in this cladogram is due in part to a distinct interpretation of male palpal bulb characters carried out in Pérez-Miles et al. (1996) cladistic analysis. For example, in this paper the character "bulbal keels smooth or absent" is considered primitive, while "bulbal keels serrated" is

considered derived for *Eupalaestrus*, *Nhandu*, *Vitalius*, *Lasiodora* and *Sphaerobothria*. However, in *Sphaerobothria* the serrated (denticulated) keel is the PI (Fig. 24), while in the other four genera, the serrated keel is the SA (Fig. 32); thus these characters are non-homologous and should be recoded. The reinterpretation of these characters surely will cause some changes to this cladogram topology.

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EXPLORING FUNCTIONAL ASSOCIATIONS BETWEEN SPIDER CRIBELLA AND CALAMISTRA

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ABSTRACT. A spider's calamistrum draws silk fibrils from its cribellum and helps combine them with supporting strands to form a cribellar prey capture thread. Despite the close functional association of these two features, this study shows that there is a great deal of variability in the ratio of cribellum width to calamistrum length. When the independent contrast method was used to examine these two features in 11 species representing seven families, no relationship was found. Likewise, no relationship was found among nine species representing seven genera of the family Uloboridae. Only among the 14 species of *Mallos* (Dictynidae) was calamistrum length directly related to cribellum width. This suggests that, above the genus level, differences in spinning behavior and morphological features such as leg length and abdomen size and shape influence the relationship of these two features.

Keywords: cribellar thread, cribellate spiders, independent contrast method, functional linkage

The outer surfaces of a cribellar capture thread are formed of thousands of fine, looped fibrils that are produced by spinning spigots on the cribellum (Eberhard & Pereira 1993; Opell 1994a, 1995, 1996; Peters 1983, 1984, 1986, 1992). These fibrils are drawn from the cribellum and manipulated by a setal comb on the fourth walking leg, termed the calamistrum, as they are combined with axial and, in some cases, paracribellar fibers to form a completed capture thread. This close functional linkage between the calamistrum and the cribellum suggests that their features should also be closely related. The most obvious features to exhibit this relationship should be calamistrum length and cribellum width. We predict that the calamistrum must be long enough to fully span the cribellum as it sweeps over it in a combing motion. However, cribellum width may not be the only factor that influences calamistrum length. The effective length of a calamistrum is probably determined by such factors as the angle at which the calamistrum passes over the cribellum and the lateral movement of the calamistrum during a combing stroke. Although these features

and their relationships are poorly studied, they are likely to be affected by the length and width of a spider's abdomen, the length of a spider's fourth legs, by the manner in which the combing leg is supported (Eberhard 1988), and probably by other details of the combing behavior such as the length of each combing stroke.

The diversity in cribellar thread-combing behavior documented by Eberhard (1988) suggests that the ratio of calamistrum length to cribellum width may differ considerably among cribellate taxa. The null hypothesis of this study is that this ratio is uniform for all cribellate taxa. Using the comparative method of phylogenetic systematics (Harvey & Pagel 1991), we test this hypothesis at three hierarchical levels: the interfamilial level, the intrafamilial level, and the intrageneric level. The degree to which differences in behavior and other aspects of anatomy influence the ratio of calamistrum length to cribellum width will affect the level at which the null hypothesis will be rejected. As behavioral and morphological features should be most similar within members of the same genus, it should be more difficult to reject the null hypothesis at this level than at more inclusive levels.

METHODS

Measurements.—The fourth legs and cribella of spiders were removed and mounted in water-soluble medium on microscope

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Table 1.—Means and standard deviations of the ratio calamistrum length to cribellum width of representative species.

Family Species	<i>n</i>	\bar{x}	SD
Uloboridae			
<i>Miagrammopes animotus</i>	31	1.35	0.10
<i>Uloborus glomosus</i>	21	1.10	0.13
<i>Octonoba sinensis</i>	24	1.27	0.11
Dictynidae			
<i>Mexitilia trivittata</i>	6	1.67	0.24
<i>Mallos bryantii</i>	5	1.55	0.25
<i>Mallo niveus</i>	9	1.58	0.27
<i>Mallos mians</i>	8	1.49	0.19

slides. Calamistrum length and cribellum width were measured to at least the nearest 20 μm under a compound or dissecting microscope. Two indices can be used for calamistrum length: the distance separating the tips of the proximal and distal-most setae of the calamistrum and the distance separating the proximal and distal-most setal bases. We chose the second index for two reasons. First, it can be more consistently measured and is not affected by missing setae. Second, it does not make any assumptions about the deflection of calamistrum setae during cribellar fibril combing. In the case of those species with divided cribella, cribellum width included the central region that separated the two halves of the cribellum. We measured a single mature female per species. We reasoned that, as the cribellum and calamistrum must be functionally linked throughout an individual's development, these measurements would provide a more rigorous test of the hypothesis than would the use of mean values derived from several individuals of a species. Table 1 gives the variance of the ratio of calamistrum length to cribellum width for seven species included in this study.

Phylogenetic analysis.—This study includes representatives of the infraorder Araneomorphae, the family Uloboridae, and the dictynid genus *Mallos* O. Pickard-Cambridge 1902 (Figs. 1–3) and uses the phylogenies of Griswold et al. (in press), Coddington (1990), and Bond & Opell (1997), respectively. To analyze the relationships of calamistrum length and cribellum width in a phylogenetic context we used the independent contrasts method of

Felsenstein (1985), as implemented by the Comparative Analysis of Independent Contrasts program of Purvis & Rambaut (1995). All branch lengths were treated as equal. This method minimizes the influence of non-independence of the data due to phylogenetic relationship by analyzing directional changes in continuous characters. It does so by computing differences between the features of sister taxa (both extant taxa and their inferred ancestors). These differences are then normalized and relationships among the resulting independent contrast values are examined using regression statistics (see Harvey & Pagel 1991 for a review of this approach).

All known species of the genus *Mallos* were included in the analysis of the relationship between the calamistrum length and cribellum width. In contrast, analyses of the other two clades included only some of the known members. We examined the consequences of partial sampling by analyzing the relationship between calamistrum length and cribellum width within subsets of the genus *Mallos*. We used a random number generator to select seven of the 14 species of *Mallos*. After constructing a pruned phylogeny that included these seven species and *Mexitilia trivittata* (Banks 1901) as an outgroup, we ran an independent contrast analysis for calamistrum length and cribellum width. This procedure was repeated until a total of ten analyses had been run. We then repeated the entire procedure a second time with nine species of *Mallos* being selected each time.

RESULTS

Values for calamistrum length and cribellum width are given in Figs. 1–3. Within the Araneomorphae, the ratio of calamistrum length to cribellum width ranged from 0.99–2.57; and an independent contrast analysis showed that there was no relationship between the dimensions of these two features ($F = 0.09$, $R^2 = 0.01$, $P = 0.77$). Within the Uloboridae the ratio of calamistrum length to cribellum width ranged from 1.07–2.06 and an independent contrast analysis showed that there was no relationship between the dimensions of these two features ($F = 0.63$, $R^2 = 0.10$, $P = 0.46$). When this analysis is restricted to orb-weaving uloborids of the genera *Waitkera* Opell 1979, *Siratoba* Opell 1979, *Uloborus* Latreille 1806, *Octonoba* Opell

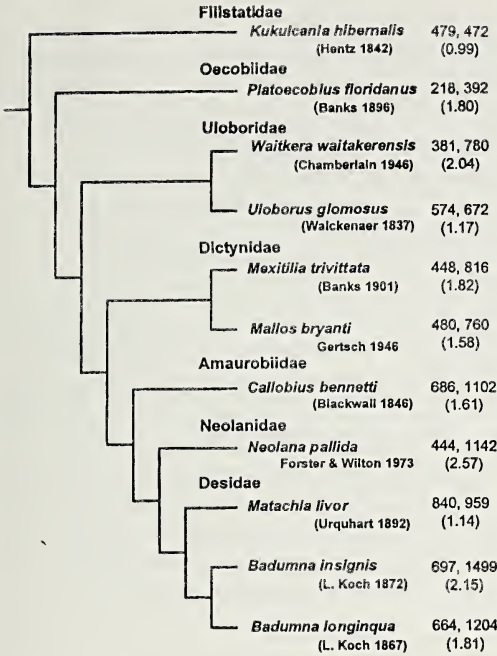


Figure 1.—Phylogeny of species representing seven families (from Griswold et al. 1999). Following each species is the width of its cribellum and the length of its calamistrum, both in μm. Ratios of calamistrum length to cribellum width are in parentheses.

1979, and *Philoponella* Mello-Leitão 1917 an independent contrast analysis still fails to show a relationship between calamistrum length and cribellum width ($F = 0.11$, $R^2 = 0.05$, $P = 0.77$).

Within the genus *Mallos*, the calamistrum length to cribellum width ratio ranged only from 1.26–1.82 and an independent contrast analysis showed that there was a relationship ($F = 8.40$, $R^2 = 0.41$, $P = 0.013$) between the dimensions of these two features (Fig. 4). However, in only three of the ten subsets that included seven *Mallos* species plus *Mexitilia trivittata* was there a significant relationship between calamistrum length and cribellum width ($F = 8.91$ – 22.75 , $R^2 = 0.64$ – 0.82 , $P = 0.005$ – 0.031). When the sample size was increased to include nine *Mallos* species, seven of the ten samples showed a relationship between these features ($F = 5.61$ – 19.95 , $R^2 = 0.45$ – 0.74 , $P = 0.050$ – 0.003).

DISCUSSION

The size of a spider's cribellum and the number of spigots that it bears are the main

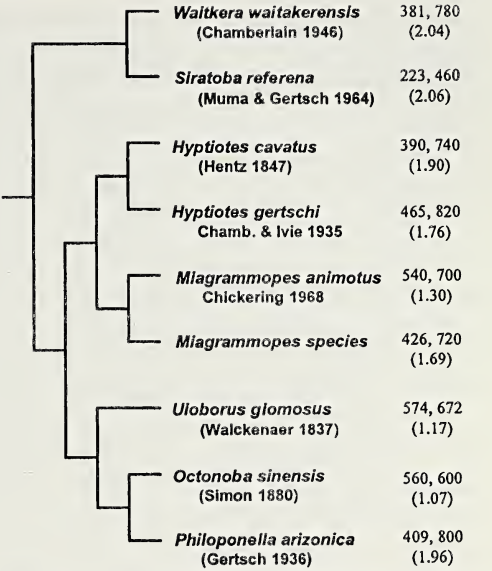


Figure 2.—Phylogeny of species belonging to the family Uloboridae (from Coddington 1990). Following each species is the width of its cribellum and the length of its calamistrum, both in μm. Ratios of calamistrum length to cribellum width are in parentheses.

factors that correlate with the stickiness of the cribellar thread that it produces (Opell 1994a, 1995, in press). However, differences in the way cribellar fibrils are combined with supporting fibers can alter thread stickiness (Opell 1994b), as can the deposition of linear cribellar threads in a looped manner when they are placed in the web (Opell, unpub. data). Although cribellum shape differs among taxa, spigot number is generally related to cribellum width. This evolutionary plasticity in cribellum width is reflected by differences in calamistrum length.

The ratio of calamistrum length to cribellum width differs among taxa; but, with one exception, it always exceeds one. In *Kukulcania hibernalis* (Hentz 1842) calamistrum length and cribellum width are essentially the same. This suggests that the production of a cribellar thread requires the calamistrum to span the complete width of the cribellum during a combing stroke. It is possible that a calamistrum could comb fibrils from only part of the cribellum spigots, but this seems unlikely for two reasons. First, as the spigots of the cribellum are probably not regionally controlled, non-calamistrum setae on other parts

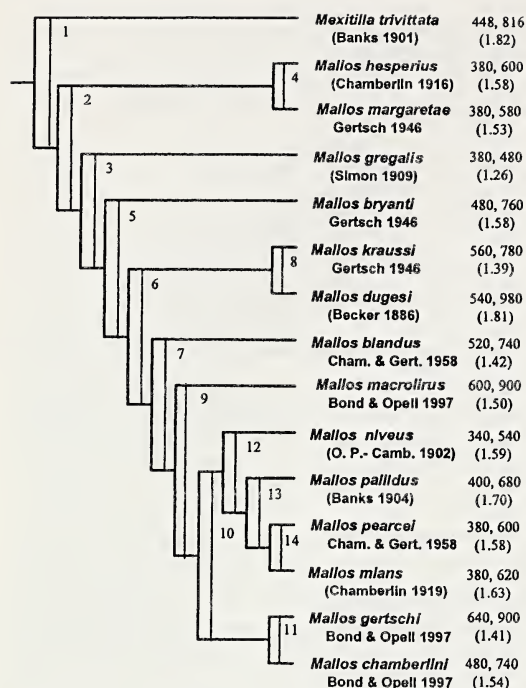


Figure 3.—Phylogeny of the 14 known species of *Mallos* and a representative of its sister group *Mexitilia* (from Bond & Opell 1997). Following each species is the width of its cribellum and the length of its calamistrum, both in μm. Ratios of calamistrum length to cribellum width are in parentheses. Numbers near vertical lines denote the sister groups whose independent contrasts are given in Figure 4.

of the combing leg that contacted cribellum spigots would tend to draw fibrils from them and these would become stuck to the leg or catch on the forming cribellar thread, thereby interfering with cribellar thread production. Second, cribellar thread is materially costly to produce (Opell 1997, 1998) and it seems unlikely that a cribellum with an unused lateral region would be retained. The apparent ease with which the cribellum itself is lost is documented by a number of families, genera, and even species pairs (putative sister species) that have both cribellate and ecribellate members (Forster 1970; Forster & Wilton 1973).

This study shows that at higher taxonomic levels, there is no uniform relationship between cribellum width and calamistrum length. This suggests that the angle at which a calamistrum passes over a cribellum or the amount of lateral movement of the calamistrum during a combing stroke differs greatly

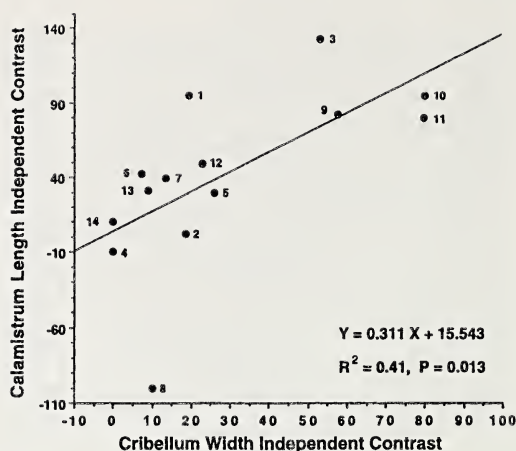


Figure 4.—Regression of independent contrast values for cribellum width and calamistrum length for 14 *Mallos* species and *Mexitilia trivittata*. Numbers identify the sister groups in Figure 3 from which these values were computed.

among spiders. As noted in the introduction, a variety of morphological and behavioral factors may influence the position and path of the calamistrum.

Even among orb-weaving species of the family Uloboridae that support the combing leg in the same manner (Eberhard 1988; Opell unpub. obs. for *Waitkera waitakerensis* (Chamberlain 1946), *Siratoba referena* (Muma & Gertsch 1946), *Uloborus glomus* (Walckenaer 1837), *Octonoba sinensis* (Simon 1880)) and share more similar body plans (abdomen dimensions, leg lengths, and ratios of leg articles; Opell 1979), the ratio of calamistrum length to cribellum width differs considerably. It is only within the genus *Mallos* that a clade-specific correlation between calamistrum length and cribellum width can be demonstrated. Even here this relationship is not exceedingly strong, as it begins to decay when sample size decreases.

As comparisons of calamistrum length and cribellum width within the family Uloboridae and among families are based on small samples, it is possible that an increased sample size would establish a significant relationship between these features. However, in comparisons of other spider features similar phylogenetic representation has been sufficient to demonstrate significant relationships (Opell 1994a, 1996, 1997, 1998, 1999, in press). Therefore, if there is a general relationship be-

tween calamistrum and cribellum features, it is weaker than those of other aspects of the phenotype.

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CHARACTERIZATION OF LIPOPROTEINS ISOLATED FROM THE HEMOLYMPH OF THE SPIDER *LATRODECTUS MIRABILIS* (ARANEAE, THERIDIIDAE)

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ABSTRACT. Two high density lipoprotein fractions (HDL₁ and HDL₂) were isolated from the hemolymphatic plasma of the spider *Latrodectus mirabilis* (Holmberg 1876). For each, the hydrated density, the electrophoresis mobility of the apoproteins, and the lipid classes composition were determined. The HDL₁ fraction carried 80% of the total plasma lipids, which were predominantly composed of phospholipids, free fatty acids, and triacylglycerols. The apoprotein composition of this fraction showed two main bands, of 90 and 103 kDa. The HDL₂ fraction was composed primarily of phospholipids, free fatty acids and cholesterol. This fraction contained hemocyanin as the principal apoprotein. When the HDL₂ fraction was separated into three subfractions, all of them contained hemocyanin, with the main subfraction containing the hexameric form of the respiratory pigment. With regard to triacylglycerol transport, lipid and apoprotein compositions and hemocyanin role in the lipid transport, these lipoproteins (HDL₁, HDL₂) show similarities and differences when compared to the two spider species already studied.

Keywords: Lipoproteins, *Latrodectus*, hemolymph

Lipids can not circulate freely in an aqueous medium due to their hydrophobicity. Notwithstanding, they are transported by hemolymph from the sites of uptake or synthesis to the sites of storage and usage via water-soluble lipoproteins. Lipid circulation systems in invertebrates have been studied only in the phyla Arthropoda and Mollusca. Although the mechanisms of lipid circulation are well-known in arthropods such as insects and crustaceans, in arachnids there is little available information on plasma lipoproteins. Lipoproteins of high density have been detected in the hemolymph of spiders, scorpions, solpugids, and mites. According to their apoprotein components, lipoproteins in spiders, scorpions, and solpugids showed similar characteristics to those of insect lipophorins (Haunerland & Bowers 1989). In spiders, the lipoprotein lipid composition was extensively studied by Haunerland & Bowers (1987) in *Eurypelma californicum* (Ausserer 1871) (Theraphosidae) and *Polybetes pythagoricus* (Holmberg 1874) (Heteropodidae) by Cunningham et al. (1994). In *E. californicum*, the high content of diacylglycerols and phospholipids also resembles the composition of insect lipophorins. In *P.*

pythagoricus, three plasma lipoproteins were detected and characterized. One of them was of high density and evidenced similar apoproteins to the ones called lipophorins. In contrast, its lipid composition was rather different, containing a large amount of phospholipids and triacylglycerols. The other two lipoprotein fractions of *P. pythagoricus*, of high and very high density, also contained phospholipids and triacylglycerols as major lipids; but hemocyanin was the predominant apolipoprotein (Cunningham & Pollero 1996).

The differences found in the lipid and apoprotein compositions of the two previously studied spiders led us to investigate the lipoproteins in a third species, *Latrodectus mirabilis* (Theridiidae), a widely distributed species. The literature reports studies on the biology and ecology (González 1981; Estévez et al. 1984) and venom components (Flo et al. 1991). There is no available study on the biochemical and physiological aspects of the lipid circulation. This study describes the composition of the lipid and protein moieties of two plasma lipoproteins isolated from the *L. mirabilis* hemolymph. The role of triacylglycerols as circulating energetic lipids, of hemocyanin

as apolipoprotein, as well as composition similarities and differences between these lipoproteins and those of other spider species, are discussed.

METHODS

Hemolymph collection and lipoprotein separation.—We collected adult females of *Latrodectus mirabilis* (deposited in the Museum of Natural Sciences, La Plata) in summer from the hills of Sierra de la Ventana, province of Buenos Aires, Argentina. After the legs were severed from the body, the spiders were placed in tubes and centrifuged at low speed in order to obtain hemolymph.

Plasma was centrifuged in a gradient density on 3 ml NaBr -1.21 g/ml, with Trasylol as protease inhibitor, at 178,000 G for 22 hours in a Beckman L8 70M centrifuge with a SW60 Ti rotor. As the density of the spider plasma was 1.006 g/ml, a saline solution of the same density was run simultaneously as blank. The total volume of the tubes was fractionated from top to bottom into 0.3 ml fractions. The density and total proteins in each fraction were monitored by refractometry and light absorption at 280 nm, respectively.

Lipid extraction and analysis.—Total lipids from the lipoprotein fractions were extracted with chloroform/methanol (Bligh & Dyer 1959). Total lipids were analyzed on Merck high performance thin-layer chromatography (HP-TLC) plates. Hydrocarbons were separated from other neutral lipids by development in hexane-benzene (70:30 v/v). Polar lipids were resolved by developing the plates in chloroform/methanol/acetic acid/water (65:25:4:4 v/v) and hexane/diethyl ether/acetic acid (80:20:1.5 v/v) for neutral lipids. Appropriate standards were used. Spots were visualized with I₂ vapors and identified by comparison with known standards.

The quantitative determination of the lipid classes was performed using a thin-layer chromatograph coupled to a flame ionization detector (TLC-FID) system. A full description of this technique was given by Ackman (1990). FID scans were performed on an Iatroscan TH-10 analyzer (Iatron Laboratories, Japan). The development solvent systems used were: hexane/benzene (70:30 v/v), benzene/chloroform/formic acid (70:25:2 v/v) and chloroform/methanol/water (70:25:3 v/v). Lipid classes were quantified by comparison

with known amounts of standards run under the same conditions and using monoacylglycerol as internal standard. Total lipids were calculated by the summation of individual lipid weights.

Gel permeation chromatography.—A very high density lipoprotein fraction separated from the gradient was analyzed under native conditions by preparative high-pressure liquid chromatography on a Superdex 200 HR 10/30 column (Pharmacia, Uppsala, Sweden) using 0.1 M Tris-HCl (pH 8.0), containing 10 mM CaCl₂ and MgCl₂, at the flow rate of 0.4 ml/min. Proteins were detected at 280 nm. Lipoprotein subfractions were eluted. The column was calibrated for molecular weight using thyroglobulin, ferritin, catalase, bovine serum albumin (BSA) and ribonuclease A (Pharmacia, Sweden) as protein markers.

Characterization of apoproteins.—Total protein concentration in each fraction isolated from the density gradient was measured colorimetrically (Lowry et al. 1951). These fractions and subfractions isolated by HPLC, were extensively dialyzed against 10 mM Tris-HCl (pH 6.8) and analyzed by electrophoresis under dissociating and native conditions. Sodium dodecyl sulfate-polyacrylamide gel electrophoresis (SDS-PAGE) was carried out in both, 8% continuous slab gels overlaid with 4% stacking gels and in gradients of 4–20% gels (Laemmli 1970) in a mini-slab electrophoresis unit (8 × 10 cm). The resolving gel buffer was 0.375 M Tris-HCl and the stacking gel buffer was 0.125 M Tris-HCl. The electrode buffer contained Tris-glycine 0.025 M Tris, 0.192 M glycine (pH 8.3). Proteins were visualized by staining with Coomassie Brilliant Blue. Molecular weight standards (HMW, Pharmacia, Uppsala, Sweden and Markerkit, Sigma Chemical Co., St. Louis, Missouri) were run in parallel lines.

The presence of hemocyanin in the fractions was monitored by spectrophotometric scans from 200–700 nm, before and after sample treatment with 0.2 M KCN solution (Nickerson & Van Holde 1971). A DW-2000 UV-Vis spectrophotometer SLM Aminco was used.

RESULTS

Isolation of plasma lipoprotein fractions.—After plasma centrifugation in density gradients, two colored bands appeared: a

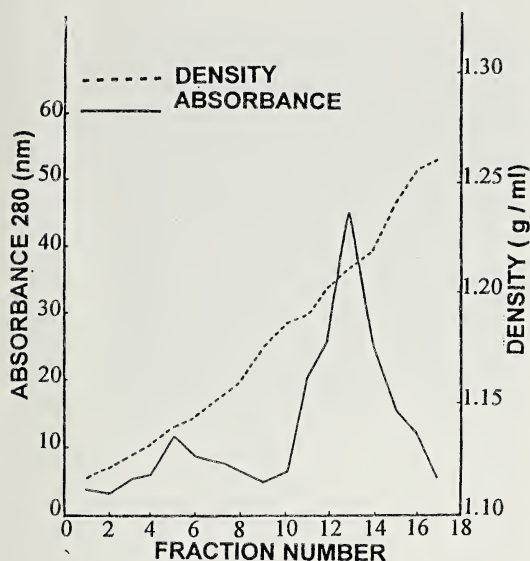


Figure 1.—Total protein (absorbance at 280 nm) and density distribution in plasma fractions of *Latrodectus mirabilis*. Plasma was centrifuged in a NaBr gradient and fractionated.

brownish one (HDL₁) and a grey one (HDL₂), whose densities were 1.13 g/ml and 1.19–1.20 g/ml, respectively. Measurements of absorbance at 280 nm performed in each fraction from gradients showed a protein profile with two maxima, one of them (the smallest) corresponded to HDL₁ and the major one to HDL₂ (Fig. 1). Plasma fractions out of colored bands showed relatively low protein and no lipid concentrations. Both colored fractions were isolated and characterized separately.

Hemocyanin was present in the HDL₂ frac-

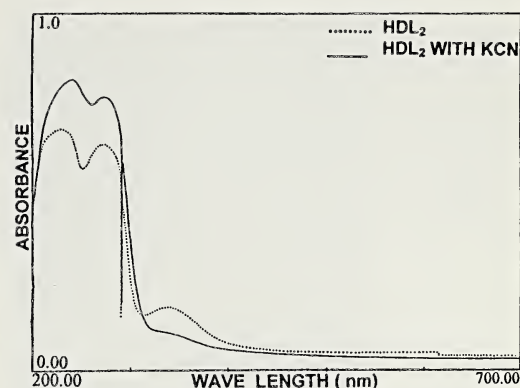


Figure 2.—Hemocyanin characterization. Spectrophotometric scans of hemocyanin from HDL₂, before and after sample treatment with KCN. Broken line = without KCN; solid line = with KCN.

tion. The respiratory pigment was identified by modification of its characteristic absorption spectrum; the absorption band of 340 nm disappeared when samples were treated with KCN solution (Fig. 2).

Lipid and protein characterization of HDL₁.—The HDL₁ carries 80.4% of the total plasma lipids. Lipids in this fraction were analyzed in their component classes. Phosphatidylcholine, phosphatidylethanolamine, free fatty acids, triacylglycerols, cholesterol and hydrocarbons were identified qualitatively using HP-TLC.

The quantitative lipid composition, determined by TLC-FID, is shown in Table 1. The predominant lipids were phospholipids (35%) and free fatty acids (33%). Triacylglycerols

Table 1.—Composition of HDL₁ and HDL₂ isolated from plasma of *Latrodectus mirabilis*. The lipoproteins were isolated by ultracentrifugation in density gradient. Lipids were identified after separation by HP-TLC and quantified by TLC-FID. Proteins were measured by colorimetry. Results are the average of three determinations (100 animals) \pm SD. Data are expressed as weight percent of lipids as determined by TLC-FID.

Component	HDL ₁	HDL ₂
Lipid classes (percent weight/weight)		
Hydrocarbons	4.0 \pm 0.3	14.1 \pm 2.3
Triacylglycerols	24.1 \pm 0.8	8.3 \pm 2.1
Free fatty acids	33.0 \pm 1.3	28.4 \pm 4.2
Cholesterol	4.2 \pm 0.3	20.1 \pm 2.7
Diacylglycerols	Traces	Traces
Phosphatidyl ethanolamine	3.6 \pm 0.2	4.0 \pm 0.5
Phosphatidyl choline	31.1 \pm 0.3	25.1 \pm 2.8
Total lipids (mg/ml hemolymph)	1.23 (20.3%)	0.3 (1.0%)
Total proteins (mg/ml hemolymph)	4.83 (79.7%)	31.6 (99.0%)

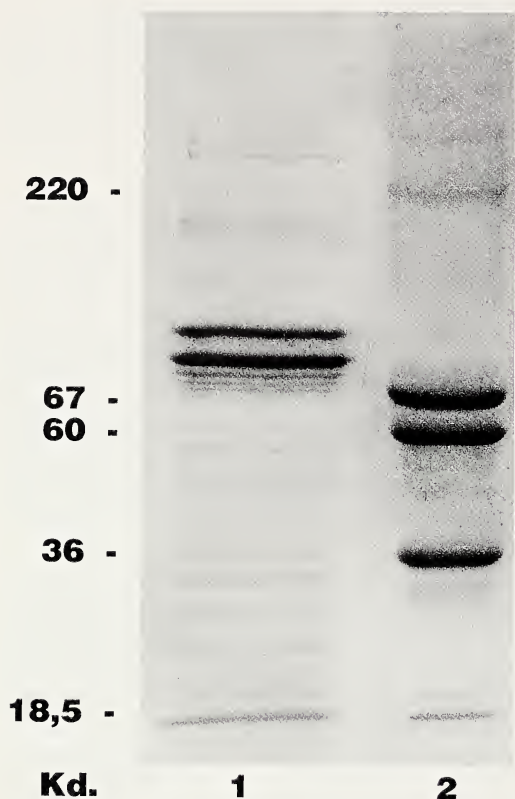


Figure 3.—SDS-PAGE analysis (4–23% acrylamide) of HDL₁ apoproteins from *Latrodectus mirabilis* hemolymph. Kd: Molecular weights of standard proteins expressed in kilodaltons. Lane 1: HDL₁ from *L. mirabilis*. Lane 2: Molecular weight standards (Kd).

were quite abundant in this fraction whereas hydrocarbons and cholesterol were found in a low proportion. Traces of diacylglycerols were also detected.

Other aliquots of HDL₁ were used to analyze the constituent apoproteins by electrophoresis. Figure 3 shows those results obtained from the electrophoretic analysis performed under dissociating conditions (SDS-PAGE). Among other proteins, two sharp bands of 90 and 103 kDa, respectively, were observed as the major HDL₁ apoproteins.

Lipid and protein characterization of HDL₂.—The HDL₂ lipids were analyzed quantitatively and qualitatively. This lipoprotein fraction carries 19.6% of total plasma lipids. The same lipid classes as those belonging to HDL₁ fraction were identified by HP-TLC and some differences were found in their rel-

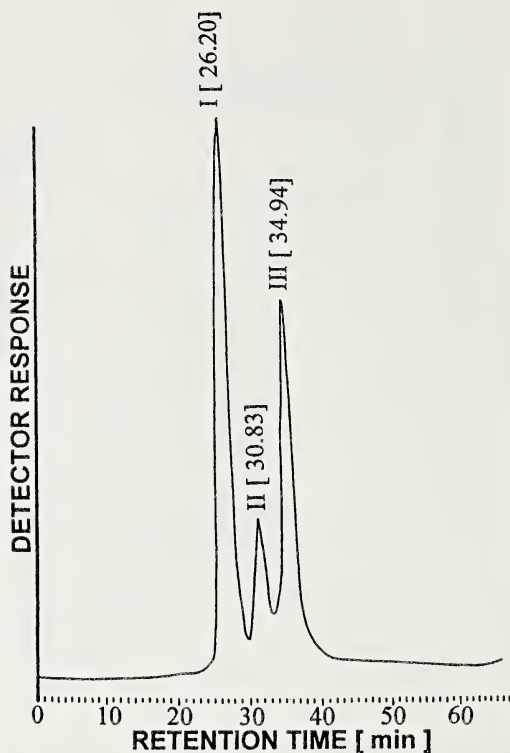


Figure 4.—Elution profile from HPLC of HDL₂ isolated from *L. mirabilis* plasma. Subfractions I, II and III were collected and analyzed separately.

ative percentages. Phospholipids (29%) and free fatty acids (28%) were the predominant lipids, followed by cholesterol, hydrocarbons and minor quantities of triacylglycerols (Table 1).

Aliquots of HDL₂ were analyzed by HPLC under native conditions using columns of molecular exclusion (Fig. 4). Three subfractions of Mr 440 kDa, 121 kDa and about 70 kDa, respectively, were found. They were eluted from the column, collected and analyzed by electrophoresis under denaturing conditions. Figure 5 (SDS-PAGE) shows two proteins of 76 and 67 kDa, respectively, in the three subfractions isolated from HDL₂.

DISCUSSION

Centrifugation in a density gradient was effective in separating two well-defined bands from *Latrodectus mirabilis* plasma which corresponded to the high density lipoproteins HDL₁ and HDL₂. HDL₁ has a density similar to that of lipophorins isolated from plasma of *Eurypelma californicum* (Hauerland & Bow-

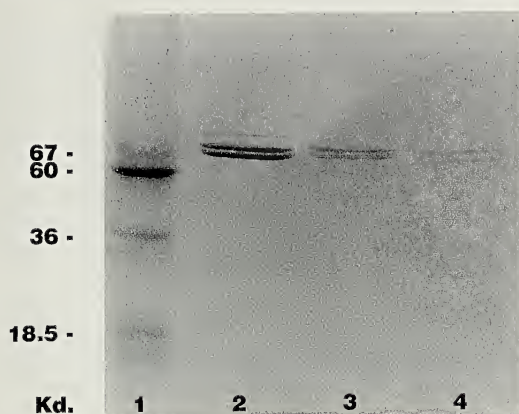


Figure 5.—SDS-PAGE analysis (4–23% acrylamide) of HPLC-fractionated HDL₂ from *Latrodectus mirabilis* hemolymph. Kd: Molecular weights of standard proteins expressed in kilodaltons. Lane 1: Molecular weight standards (Kd). Lane 2: HDL₂ subfraction I. Lane 3: HDL₂ subfraction II. Lane 4: HDL₂ subfraction III.

ers 1987) and of *Polybetes pythagoricus* (Cunningham et al. 1994), which are the only arachnids which have been studied in detail. Its density is also similar to that of lipophorins found in insects (Chino et al. 1981). The HDL₂, though its density is greater than the HDL₁ fraction, is also a high density lipoprotein, and so it can be compared to the HDL previously isolated from plasma of *P. pythagoricus* (Cunningham & Pollero 1996).

HDL₁ is the main lipid carrier fraction in *L. mirabilis* hemolymph since more than three-fourths of the total plasma lipids are associated to it. This quantitative importance in lipid transport locates it at the same level as that of *E. californicum* and above *P. pythagoricus* lipophorin which only carries about 30% of circulating lipids. In contrast, when lipid classes found in this lipoprotein fraction are compared, similarities to *P. pythagoricus* and differences to *E. californicum* are evident. Phospholipids and fatty acids are the predominant lipids; and, as in *P. pythagoricus* lipophorin, triacylglycerols are the most abundant neutral lipids. This fact indicates that triacylglycerols together with free fatty acids are the main circulating energetic lipids in this species, in contrast to *E. californicum* and insects where the presence of large amounts of diacylglycerols characterizes the lipophorins.

The protein moiety of HDL₁ is composed of two principal polypeptides with a molecu-

lar weight of 90 and 103 kDa, respectively. This also differs when compared to *E. californicum* and *P. pythagoricus* apolipophorins, and to those found in other arachnids whose protein moieties have been studied (Haunerland & Bowers 1989). In all these cases as well as in insects, lipophorin particles contain apoproteins of 80 and 250 kDa and a total weight of about 500 kDa. In short, due to its composition, the HDL₁ of *L. mirabilis* is significantly different when compared to HDLs of the same density in other invertebrates that are taxonomically close to it. For this reason, we think it shouldn't be named lipophorin.

In *L. mirabilis*, the HDL₂ could play a secondary role in the hemolymph transport of lipids due to the fact that the lipids associated to this lipoprotein are lesser than those ones bound to the HDL₁. Nevertheless, its lipid composition, with relatively high amounts of hydrocarbons and cholesterol, suggests that HDL₂ could be specialized in the transport of these lipid classes. Although this lipoprotein particle differs from the HDL of *P. pythagoricus* not only in the lipid/protein ratio but also in the lipid classes it transports, both of them carry triacylglycerols but no diacylglycerols as the main neutral acylglycerides.

The electrophoretic analysis of HDL₂ under dissociating conditions, shows protein bands with molecular weights similar to the hemocyanin monomers found in other spiders (Schneider et al. 1977; Lamy et al. 1979; Markl 1986). The removal of copper by KCN treatment confirms this identification. Although we tried to stabilize the hemocyanin, it is very likely that, when handling the samples, there would have been some dissociation of HDL₂ native particles; and, consequently, subfractions of different size would have appeared after gel permeation chromatography. The loss of native conformation of hemocyanin could be the result of changes in the pH, the divalent cation concentration during the processing samples, or due to the use of NaBr in the centrifugation procedure (van Holde & Miller 1986; Hepskovits & Villanueva 1986; Herskovits et al. 1991).

Undoubtedly hemocyanin plays an apolipoprotein role since it is part of this lipoprotein particle as a principal protein. This function of hemocyanin in spiders regarding the lipid transport, in addition to its classical role as respiratory pigment, has been recently re-

ported for *P. pythagoricus* plasma (Cunningham & Pollero 1996) where, however, other polypeptides associated with hemocyanin were also found. In this study, the three sub-fractions isolated from *L. mirabilis* HDL₂ under dissociating conditions only yielded hemocyanin monomers. This corroborates the apoprotein function of hemocyanin in this lipoprotein. This apolipoprotein role of hemocyanin is not a constant in spiders, since no associated lipids could be detected in tarantula hemocyanin. A similar finding has been reported for molluscs where the hemocyanin of the cephalopod *Octopus tehuelchus* transports lipids (Heras & Pollero 1992), while that of the gastropod *Ampullaria canaliculata* does not (Garin & Pollero 1995).

In *P. pythagoricus* plasma, we have characterized a third lipoprotein of very high density which is the main carrier of circulating lipids, and which contains hemocyanin as the principal apoprotein (Cunningham & Pollero 1996). The existence of a VHDL has also been reported for *Eurypelma californicum* (Haunerland & Bowers 1989). In this case, however, it was a lipoprotein without hemocyanin which played a secondary role in lipid transport. In *L. mirabilis* no particle with VHDL characteristics has been detected.

In brief, *L. mirabilis* contains two plasma lipoproteins; but their lipid and protein compositions share only a few features with the hemolymph lipoproteins already described other spider species. Such differences in number and composition of plasma lipoproteins in taxonomically close organisms make generalization difficult.

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DIET-INDUCED AND MORPHOLOGICAL COLOR CHANGES IN JUVENILE CRAB SPIDERS (ARANEAE, THOMISIDAE)

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ABSTRACT. The effect of dietary pigments on abdominal color of juvenile spiders was examined in the laboratory using the flower-dwelling crab spiders *Misumenops asperatus* (Hentz 1847), *Misumenoides formosipes* (Walckenaer 1837), and *Misumena vatia* (Clerck 1757) (Thomisidae). Because these species lack hypodermal chromes, ingested prey pigments may show through the epidermis and affect opisthosomal coloration. Diet-induced color changes were restricted to the opisthosoma, and all three spider species responded similarly to dietary pigments. Opisthosomas of instars 2–4 fed red-eyed fruit flies turned pink, and the pink color faded back to the normal white over a period of 4–6 days. Opisthosomas of instars 5–7 fed red-eyed fruit flies remained white, as did opisthosomas of all instars fed white-eyed fruit flies (controls). In a field population of *M. asperatus*, 82% of spiders in July (instar 2), 93% of spiders in August (instars 3–4), and 8% of spiders in September (instar 5) had pink, orange, or brown opisthosomas. Yellow juveniles were also seen: 5% and 57% of *M. asperatus* observed in August and September, respectively, were yellow. Yellow juvenile *M. formosipes* were observed in the field as well. The yellow color did not result from dietary pigments, but was, rather, a morphological color change and included the prosoma and limbs, as well as the opisthosoma.

Keywords: Flower spiders, opisthosoma, prey pigments, size-dependent effect

The ability of certain species within the family Thomisidae (crab spiders) to undergo a reversible color change depending on their environmental substrate, a process referred to as a morphological color change (Holl 1987), has provoked interest among naturalists since the late nineteenth century (Angus 1882; Packard 1905; Gadeau de Kerville 1907; Gabritschewsky 1927; Gertsch 1939; Weigel 1941). Most investigations of morphological color changes among thomisids have focused on the goldenrod spider, *Misumena vatia* (Clerck 1757) (e.g., Packard 1905; Gabritschewsky 1927; Millot 1926; Weigel 1941), and the ability to change color has been attributed only to adult females (Gabritschewsky 1927).

Misumena vatia is typically white, but turns yellow when placed on a yellow substrate. Because this species lacks hypodermal chromes and has a translucent cuticle, reflection of white light from guanine crystals in the intestinal diverticula causes *M. vatia* to appear

white (Millot 1926; Weigel 1941). Under the stimulus of reflected yellow light (Gabritschewsky 1927; Weigel 1941), a yellow pigment is released into the hypoderm (Weigel 1941), and the yellow color becomes more intense the longer a spider remains on a yellow substrate (Packard 1905; pers. obs.). Morphological color changes involve a spider's entire body: prosoma, opisthosoma, and limbs take on a yellow hue. Similar morphological color changes have been reported in other thomisid species, including *Misumenoides formosipes* (Walckenaer 1837) and *Misumenops asperatus* (Hentz 1847) (Gertsch 1939; Schmalhofer 1996).

Having a colorless, translucent integument has an interesting side-effect on juvenile flower-dwelling crab spiders: ingested material that is strongly pigmented may show through the epidermis, changing the color of a spiderling's opisthosoma. In the field, juvenile crab spiders having pink, orange, brown, green, yellow, or white opisthosomas have been observed (Schmalhofer 1996). Peck & Whitcomb (1968) observed similar diet-induced color changes in the clubionid *Cheiracanthium inclusum* (Hentz 1847), a pale yellow

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spider with a transparent integument. They noted that spiders turned green and pink when fed pyralid larvae and red-eyed *Drosophila*, respectively; and they obtained a variety of opisthosomal colors by feeding spiders an artificial diet containing dye (Peck & Whitcomb 1968). No information was provided, however, concerning how long color changes lasted, their frequency of occurrence under natural conditions, or the instars affected. Using flower-dwelling crab spiders, I performed a laboratory experiment to determine the duration of diet-induced color changes and the instars affected. Field observations were also conducted to determine the frequency of occurrence of diet-induced color changes in a natural crab spider population.

METHODS

Effects of *Drosophila* eye pigments on opisthosomal color of juvenile crab spiders.—The effect of *Drosophila* eye pigments on opisthosomal color of juvenile crab spiders was examined using *M. asperatus*, *M. formosipes*, and *M. vatia*. Adults of the three species are seasonally separated. *Misumenops asperatus* matures and females lay a single egg sac in spring, and spiderlings emerge in early summer and overwinter as late instar juveniles (pers. obs.). *Misumenoides formosipes* matures in midsummer, females produce a single egg sac in late summer or early autumn, and spiderlings generally overwinter in the egg sac (pers. obs.). *Misumena vatia* matures and females produce a single egg sac in early-to-midsummer, and spiderlings emerge in late summer and overwinter as middle-instar juveniles (Fritz & Morse 1985). These species have seven juvenile instars, the first of which is spent in the egg sac (Gertsch 1939).

Misumenops asperatus and *M. formosipes* were reared from egg sacs produced by females collected in Middlesex and Somerset Counties, New Jersey. Adult specimens of *M. asperatus* and *M. formosipes* have been deposited at the American Museum of Natural History. I have never found *M. vatia* in New Jersey, although the species is recorded as occurring in the state (Gertsch 1939). *Misumena vatia* used in the laboratory experiment originated in Lincoln County, Maine, and egg sacs were provided by D. Morse. Egg sacs were maintained at room ambient temperature (25–30 °C); and, after emergence, second instar

spiderlings were placed in separate 4 dram shell vials with cotton plugs. Spiders were starved for seven days prior to a feeding trial to ensure that their guts were empty (Anderson 1970; Nakamura 1987). During a feeding trial, a spider was supplied with either 10 red-eyed fruit flies (experimental group) or 10 white-eyed fruit flies (control group). Any flies not consumed after five hours were removed. After feeding, a spider's opisthosomal color was subjectively categorized as bright pink, moderately pink, pale pink, or white. The number of days required for a spider's opisthosoma to return to the normal white color was also noted. This protocol was repeated during each juvenile instar (instars 2–7) for each species. The number of spiders used in a feeding trial varied with species and instar ($n = 6$ –20).

Natural occurrence of juvenile *Misumenops asperatus* having colored opisthosomas.—Field observations focused on *M. asperatus* and took place in a 2.8 ha² field adjacent to the Busch campus of Rutgers University in Middlesex County, New Jersey. I tagged 250 inflorescences each of *Achillea millefolium* (yarrow), *Daucus carota* (Queen Anne's lace), and *Solidago* spp. (goldenrod), which were plant species commonly used by *M. asperatus* (Schmalhofer 1996). *Solidago* was the dominant plant species in the field, occupying approximately 76% of the area and having a density of 55.4 stems per m². *Achillea* patches were interspersed among the *Solidago* and covered approximately 6% of the area. *Achillea* had a density of 31.7 stems per m². *Daucus*, with a density of 16.6 stems per m², occurred at the field perimeter and covered approximately 14% of the area. Blooming in *Achillea*, *Daucus*, and *Solidago* occurred sequentially over the course of the summer, and flowering phenology in the three species showed little overlap (pers. obs.). Flowering in *Achillea* occurred from early June to mid-July, flowering in *Daucus* occurred from mid-July to mid-August, and flowering in *Solidago* occurred from mid-August through September. Over seven consecutive days at the beginning of July, August, and September, I made daily surveys of tagged *Achillea*, *Daucus*, and *Solidago*, respectively. Observations occurred between 0900–1200 h, and I recorded the number of spiders per inflorescence and spider color.

RESULTS

Effects of *Drosophila* eye pigments on opisthosomal color of juvenile crab spiders.—

Misumenops asperatus, *M. formosipes*, and *M. vatia* responded similarly to *Drosophila* eye pigments. When fed red-eyed fruit flies, only a spider's opisthosoma changed color: prosoma and legs were unaffected by dietary pigments. I found that the opisthosomas of instars 2–4 fed red-eyed *Drosophila* turned pink, and the pink color slowly faded to the normal white over a period of 4–6 days. Intensity and duration of the color change varied with age of the spider. Second instar spiders turned bright pink, while older spiders took on a pale-to-moderate shade of pink. Intensity of opisthosomal color in instars 3–4 also seemed to vary with the number of *Drosophila* consumed: spiders capturing a single fly turning pale pink, while those capturing multiple prey (2–3 flies) took on a darker hue. Few spiders captured more than one fly. Opisthosomal color of older instars returned to normal more quickly (4 days) than did that of younger spiders (6 days). Opisthosomal color of instars 5–7 was not affected by *Drosophila* eye-pigments, regardless of the number of flies consumed. Opisthosomas of all spiders in the control groups fed white-eyed *Drosophila* remained white.

Anecdotal observations indicated that the intensity and duration of dietary color changes and instars affected were also influenced by the causative pigment. For instance, the opisthosoma of an instar 5 *M. asperatus* that consumed a blood-fed mosquito turned dark brown, and the color faded over a six-day period. Opisthosomas of instars 4–5 of *M. asperatus* found in the field feeding on unidentified green hemipterans turned brilliant green, but returned to normal after only two days.

In all three species, spider size changed by more than an order of magnitude during the juvenile period. Mass of instar 2 spiders was less than 1 mg, while average mass of instar 7 (penultimate) female spiders was much greater: 48 mg (*M. vatia*, calculated from Fritz & Morse 1985; Morse 1988; Morse & Stephens 1996), 42 mg (*M. formosipes*), and 24 mg (*M. asperatus*).

Natural occurrence of juvenile *Misumenops asperatus* having colored opisthosomas.—The proportion of spiders showing di-

etary color changes was very high in July and August (Table 1), and pink or orange opisthosomas were the most commonly seen variations. The yellow color observed in juvenile *M. asperatus* in August and September was not dietarily induced, but was, rather, a morphological color change like that described for adult spiders (see introduction). The effects of dietarily acquired pigments were restricted to the opisthosoma, but yellow juveniles were fully colored; prosoma and limbs, as well as the opisthosoma, were yellow. Both male and female spiderlings were observed to turn yellow. Juvenile *M. formosipes* also proved capable of undergoing a morphological color change; 8% of juveniles seen in July (instars 5–6) and 50% of juvenile females seen in August (instar 7) were yellow. I have also observed yellow *M. formosipes* in sweepnet samples collected earlier in the season (May and June). The seasonal increase in the proportions of yellow juveniles in both *M. asperatus* and *M. formosipes* populations reflected an increase in the availability of plant species with yellow flowers (predominantly *Solidago*) during the course of the summer.

Spider position on inflorescences varied with plant species. On *Achillea*, most *M. asperatus* were found on the underside of inflorescences; on *Daucus*, spiders occurred with similar frequencies on the upper surface and the underside of inflorescences; and on *Solidago*, most spiders wedged themselves between the individual flowers comprising an inflorescence. Having a colored opisthosoma did not appear to influence spider position on inflorescences of any of the plant species examined. This observation, however, was not quantified.

DISCUSSION

Although opisthosomal color provides some clues as to a juvenile crab spider's recent feeding history, opisthosomal color should not be used as a means of categorizing juveniles in field populations as hungry or satiated. Too many variables affect opisthosomal color (e.g., number of prey ingested, spider age, time since ingestion, causative pigment, etc.) to make opisthosomal color a reliable indicator of hunger status. Also, many prey types captured by flower-dwelling crab spiders lack strong pigments and, thus, would not affect spider color.

Table 1.—Proportions of *Misumenops asperatus* of various colors seen during the summer months in central New Jersey. Values presented are averaged over the seven days of observations each month. Spider densities are presented as mean number of spiders per inflorescence (\pm 1 SD); 250 inflorescences of each plant species were surveyed. Flower color is indicated below each plant species. Spider colors marked with an * are diet-induced.

Month	Plant species	Instar	Spider density	Spider color				
				White	Yellow	Pink*	Orange*	Brown*
July	<i>Achillea millefolium</i> (white)	2	0.09 (0.06)	0.18	0.00	0.82	0.00	0.00
August	<i>Daucus carota</i> (white)	3–4	0.83 (0.11)	0.01	0.05	0.50	0.38	0.05
September	<i>Solidago</i> spp. (yellow)	5	0.07 (0.03)	0.35	0.57	0.01	0.07	0.00

The effect of dietary pigments on flower-dwelling crab spiders appears to be limited by spider size: smaller (younger) juveniles show the effects of prey pigments, while larger (older) juveniles are generally unaffected. Like older juveniles, adult females are unaffected by prey pigments (pers. obs.): mature female spiders fed red-eyed fruit flies *ad libitum* in the laboratory never displayed opisthosomal color changes, nor have I ever observed adult females in the field to be affected by pigments of ingested prey. In contrast to female crab spiders, adult males are small, typically 5 mg or less (Morse & Stephens 1996; pers. obs.). Because adult *M. vatia* and *M. asperatus* males largely lack opisthosomal chromes, abdominal color in males of these species has the potential to be affected by diet. However, this seems to be a rare occurrence. During eight years of field research, I have observed only a single adult male *M. asperatus* showing dietary pigments. The opisthosomal hypoderm of adult male *M. formosipes* contains yellow chromes, which would obscure any ingested pigments. Thus, mature male *M. formosipes* are not subject to diet-induced color changes.

The differential effect of prey pigments on younger vs. older spiders, as seen in the laboratory experiment, can be explained by gut volume and feeding habits. Crab spiders begin feeding from their prey's head (Pollard 1989, 1993; pers. obs.); therefore, eye pigments are ingested early during feeding. Compared to older (larger) spiders, younger (smaller) individuals have correspondingly small gut capacities and their smaller stomach muscles probably exert less force during feeding (this was not tested). Consequently, younger spiders ex-

tract less material from a given prey item than do older spiders, and eye pigments compose a larger fraction of the ingested food. The tendency of crab spiders to discard one prey item before all the available material has been extracted and to begin feeding on a new prey item when prey is abundant (Pollard 1989) may have enhanced the effect of *Drosophila* eye pigments on opisthosomal color of younger juveniles. When offered an abundance of prey, Pollard (1989) found that crab spiders discarded the original prey item after a period of time corresponding to the length of time spent feeding from the head when only one prey item was provided.

Morphological color changes in crab spiders are erroneously described as being restricted to adult female spiders (Gabritschewsky 1927; Gertsch 1939; Hinton 1976; Holl 1987). This assertion is based on Gabritschewsky's (1927) experiments with laboratory-reared *M. vatia*, and does not hold true for *M. asperatus*, *M. formosipes*, or natural populations of *M. vatia*. In the field, juvenile *M. vatia* have been observed to undergo morphological color changes (D. Morse pers. commun.). It is possible that Gabritschewsky's results were due to the restricted diet (*Drosophila*) given to the spiderlings or to some other difference between the laboratory and field environment (e.g., light intensity, substrate character). Light quality or intensity in particular may be important in effecting morphological color changes: compared to color changes occurring under natural conditions, color changes occurring under artificial lighting take longer to complete and a paler yellow hue results (pers. obs.).

The ability to turn yellow has obvious benefits for juvenile (and adult) crab spiders. By enhancing crypsis on yellow flowers, yellow spiders are less likely to be detected by predators or prey. This capability would be particularly useful for juvenile spiders if a large portion of the juvenile period coincided with a seasonal increase in the availability of yellow-flowered plant species, as occurs in *M. asperatus*. Conversely, the impact of dietary color changes on crab spider fitness parameters, such as prey capture success and susceptibility to predators, is unknown, but presumably would be negative. At the study site, most plant species available in early-to-mid-summer had white flowers. Therefore ingested prey pigments could cause a spiderling to contrast strikingly with its floral substrate. However, since pink and orange were the predominant opisthosomal colors, apparency to insects may not have been strongly affected. Most insects are considered to be red-blind (Borror et al. 1989; Barth 1991), but this interpretation of insect visual systems has recently been challenged (Chittka & Waser 1997). Susceptibility to visual predators with good color perception/discrimination, such as birds, could be enhanced by spider ingestion of prey pigments. Further studies are needed to determine what, if any, impact diet-induced color changes have on crab spider fitness parameters.

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COSTS AND BENEFITS OF FORAGING ASSOCIATED WITH DELAYED DISPERSAL IN THE SPIDER *ANELOSIMUS STUDIOSUS* (ARANEAE, THERIDIIDAE)

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ABSTRACT. In the theridiid spider, *Anelosimus studiosus*, most juveniles remain in their natal web, forming temporary colonies in which individuals cooperate in web maintenance and prey capture until they disperse at maturity. There is natural variation in age at dispersal, and subadult spiders removed from their natal webs build webs and continue to develop. To explore the costs and benefits of delayed dispersal, we compared the rate of prey capture and developmental rate for individuals in colonies and those isolated at the fourth instar. Rate of prey capture by colonies increased with colony size and age; this result was driven primarily by the enhanced capture of large prey by larger and older colonies. The presence of juveniles increased the overall productivity of webs, an effect which remained after the juveniles were removed from the web. Despite the overall increase in prey capture, per-individual prey capture decreased with colony size. The variance in prey capture success decreased significantly with colony size, but not with colony age. Spiders in colonies captured more prey per juvenile than singletons experimentally dispersed at the fourth instar; however, this did not result in increased development rate of colonial juveniles over isolated juveniles. These data suggest that juvenile *A. studiosus* benefit from delayed dispersal by acquiring more resources and acquiring them more steadily. The productivity of webs of females whose juveniles were removed at the fourth instar remained higher than those of similarly aged females who never produced juveniles. This suggests that delayed dispersal of juveniles enhances the resources which the female could allocate to her next egg mass.

Keywords: Parental investment, sub-sociality, risk-sensitivity, cooperative foraging

Because spiders are generally limited by resources (Wise 1993), it is likely that any resources a mother spider provides to her juveniles would reduce her future egg production. Thus the behavior of maternal social spiders would fit Trivers' (1972) definition of parental investment, in which a mother's behavior enhances the survival of her current brood, at a cost to her production of future broods. However, if juveniles remain in their natal webs beyond an early altricial phase and become active in the web, their continued presence may enhance prey capture and/or defense. This in turn could enhance the mother's production of future broods. In this way a mother may recoup her initial parental investment in terms of future reproductive success. The objective of this work is to describe the relative costs and benefits of delayed dispersal in *Anelosimus studiosus* (Hentz 1850), a spider in which the maternal-juvenile association is longer than in most maternal social species. We used laboratory ex-

periments to examine the effects of delayed dispersal on prey capture and development rate of late instar juveniles. We also examined the post-dispersal prey capture of webs in order to determine if delayed juvenile dispersal could enhance a mother's future reproductive success.

The effect of maternal care on the survival and growth of juveniles in maternal social spiders is well documented. Guarding of egg sacs is a relatively common form of maternal care in spiders, providing protection from predation and parasitism (Foelix 1996). In colonies of the theridiid spider *Theridion pictum* (Walckenaer 1802), unguarded egg sacs had drastically reduced hatching success, but juvenile size was not affected (Ruttan 1991). In about 20 described species, mothers actively provision their offspring with paralyzed or regurgitated prey (Foelix 1996). Mothers of the European agelenid spider *Coelotes terrestris* (Wider 1834) provision their offspring and protect them from predators and parasites un-

til the juveniles disperse after about one month (Horel & Gundermann 1992). Under laboratory conditions, the mother's presence had a significant positive effect on juvenile survival. The mother's parental investment, in terms of her ability to produce a second brood, was small relative to the enhanced survivorship of the current brood (Gundermann et al. 1997).

The 17 known species of non-territorial permanent-social spiders represent six families and are mostly found in the tropics (Avilés 1997). Several studies have indicated that individual survivorship of colony members is greater than that of solitary individuals (Christenson 1984; Riechert 1985; Avilés & Tufiño 1998). Potential benefits of group living for spiders include reduced individual silk costs (Riechert et al. 1985; Tietjen 1986), capturing larger prey (Nentwig 1985; Rypstra 1990; Rypstra & Tirey 1990; Pasquet & Krafft 1992) and reduced predation (Henschel 1998). Fecundity in social spiders is lower than in solitary species (Riechert 1985; Vollrath 1986; Wickler & Siebt 1993). Female *Anelosimus eximius* in large colonies have lower fecundity than those in intermediate colonies (Keyserling 1884, Avilés & Tufiño 1998). Potential costs of sociality for spiders include competition within the group (Rypstra 1993), increased incidence of parasitism (Avilés & Tufiño 1998), and susceptibility to diseases (Henschel 1998).

The social behavior of the theridiid spider, *A. studiosus*, is intermediate between the maternal social and the non-territorial permanent-social spiders (Brach 1977), and the costs and benefits of delayed juvenile dispersal may go beyond simple parental investment. If web productivity is sufficiently enhanced by the presence of the late-instar, participating juveniles, this enhancement could balance the costs of parental care to the mother, or even enhance her production of future broods. In this regard, *A. studiosus* may represent an evolutionary intermediate between maternal social and non-territorial permanent-social spiders and, thus, could provide an important link in understanding the evolution of spider sociality.

METHODS

Study species.—*Anelosimus studiosus* range from Argentina to New England and are

typically found in open habitat, building webs at the tips of branches in low shrubs (Brach 1977). Adult females are fertilized before leaving the natal web or shortly after dispersal. The mother produces and guards an egg case, feeds newly-emerged offspring through regurgitation, and provides second instar juveniles with paralyzed prey. As the juveniles develop beyond the second instar, they participate increasingly in prey capture and web maintenance (Brach 1977). Juveniles isolated at the fourth instar or later can build their own webs, capture prey and continue to develop (Brach 1977; pers. obs.). Males are mature at the sixth post-emergent instar, and females at the seventh (pers. obs.). As the juvenile females mature, the mother becomes aggressive towards them, forcing them from the web (Brach 1977; but see Furey 1998). Adult males are always tolerated in the web by the mother; therefore, the maturing males apparently disperse of their own accord (Brach 1977). Female *A. studiosus* can produce up to three consecutive broods using the same web (pers. obs.).

Rearing methods.—We collected 16 colonies from the Ocala National Forest in Florida in 1994 and 1995. We reared these colonies on live shrubbery within a 3.6 m × 2.4 m × 2.1 m enclosure in the Biological Sciences Greenhouses located at The Ohio State University, maintained at temperatures between 23–32 °C, with a combination of natural light and supplemented light (on cloudy days) reflecting the natural light cycle. Flying prey (*Musca domestica*, *Drosophila melanogaster* and *D. hydei*) were released into the enclosure three times a week, at which time the colonies were misted with distilled water. From the enclosure, we collected 72 adult females dwelling singly in newly-constructed webs in late March and early April 1997 and maintained them individually in 500 ml plastic containers. Each spider was provided a coiled twist-tie, which they used as a retreat. We fed them *ad libitum*, misted them three times a week, and exposed them to a male for 24 h within the week after they were collected. Voucher specimens are placed in The Museum of Biological Diversity at The Ohio State University.

Experimental procedure.—Thirty-eight of the 72 isolated females produced egg cases. We placed these, with their egg sacs and retreats, onto a small piece of artificial shrub-

bery for 24 h while they constructed new webs. We then wired these new webs into the middle of larger arrangements of artificial shrubbery which were standardized by number, size and positioning of the leaves. We housed the webs, individually, within cuboidal enclosures 46 cm on a side (these were screened on the four sides and solid on the top and bottom). Three times a week, we misted the webs and released two *M. domestica* and ten *D. melanogaster* into the enclosure. We censused each web 48 h after prey release for the numbers and types of prey captured, as well as the numbers and age classes of juveniles present in the web. We removed the carcasses of captured prey from the webs and enclosures after each census.

We assigned webs to two groups. In the treatment group we removed the juveniles from their natal web when the majority of them had reached the fourth instar, and individually placed three of the juveniles as singletons into the experimental conditions described above. In the control group we removed the juveniles similarly, but immediately replaced them and allowed them to develop and disperse naturally. We assigned webs to the two groups by first ranking them in order of number of juveniles in the web, then flipping a coin to decide the treatment of the first web, alternating the assignment of the remaining webs thereafter. We did this to ensure a fair representation of the range in number of juveniles in each treatment. There was no juvenile mortality or dispersal over the period for which the results are reported; thus, the number of juveniles remained constant within colonies.

Seventeen females without juveniles were maintained under the experimental conditions for comparison with webs of similar age containing juveniles. Of these, ten did not produce egg sacs, and seven produced egg sacs that did not hatch. If any of the adult females died during or within a week after the experimental period, we did not include data from their webs in the analyses. Twenty of the 38 egg sacs produced did not hatch, and six of the mothers died during the experiment. Data from seven control webs and five experimentally-dispersed webs were used.

We estimated the amount of extractable resources for a given prey type as the average wet weight minus its average dry weight (13.1

mg for houseflies, 0.4 mg for *Drosophila*). Prey capture success was recorded as the number of each prey type times their extractable weight. Due to asynchronous juvenile development, the age class of a web was described by the instar of the majority of the juveniles in it.

Data analysis.—In analyses exploring how colony size affects the amount of prey captured, we calculated the mean per-trial prey capture over the period that juveniles were present. We estimated the per-juvenile prey capture by dividing the total mass of prey captured in a trial by the number of juveniles in the colony. To analyze how colony size affects variation in prey capture, we used the coefficient of variation (CV) among trials within colonies, in per-juvenile prey capture. We chose CV to standardize for the fact that we expect the variance to increase as the mean increases. We used regression analyses on the means and CVs of the colonies to test for effects of colony size. In analyses of effects of colony age on foraging success we used data from the colonies multiple times (means and CVs at each instar within colonies), resulting in non-independence of the data. To account for this, we performed repeated measures analyses of covariance, with the instar of the majority of the juveniles as the covariate, and the individual colony as a random factor.

RESULTS

Effects of delayed dispersal on prey capture.—Across all webs, prey capture increased significantly with juvenile age (Fig. 1). In this plot, data from both the treatment and control colonies are factored into the means of the first three instars, because at that point both sets were intact and undisturbed. Only the control colonies are factored into the means of fourth through sixth instars. However, we used only data from the control colonies in the repeated measures ANCOVA. Mean per-trial prey capture also increased significantly with number of juveniles in the colony (Fig. 2). Despite the overall increased productivity of larger webs, there was less prey available to individual spiderlings as the number of juveniles increased (Fig. 3). The average coefficient of variation in per-juvenile prey capture showed no trend with respect to colony age (Fig. 4). There was, however, a significant decrease in the coefficient of vari-

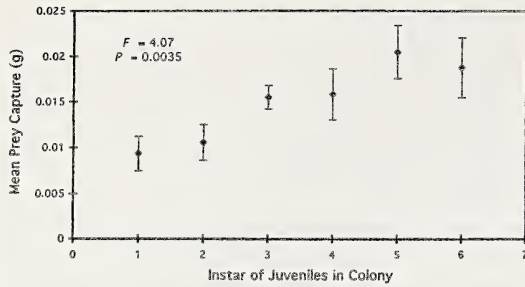


Figure 1.—Average per-trial prey capture during the period juveniles were in the web vs stage of the colony. Plotted are the means for the colonies at a given instar with standard error bars (repeated measures ANCOVA $F = 4.07$, $P = 0.0035$).

ation in per-juvenile prey capture as colony size increased (Fig. 5).

Much of the effects of colony size and age on foraging success were driven by the enhanced ability of larger and more mature colonies to capture the larger prey items. The average number of houseflies captured per trial increased significantly with colony size ($R^2 = 0.79$, $P = 0.007$; regression of the average number of houseflies captured per trial on the log of the number of juveniles in the colony). This increase was non-linear and asymptotic because the larger colonies depleted the available flies. There was also a significant increase in the mean number of houseflies captured with colony age ($F = 2.69$, $P = 0.04$; repeated measures ANCOVA with juvenile instar as a cofactor).

Effects of delayed dispersal on juvenile development.—The development rate of juveniles in colonies, as measured by the amount of time required to reach the fourth or

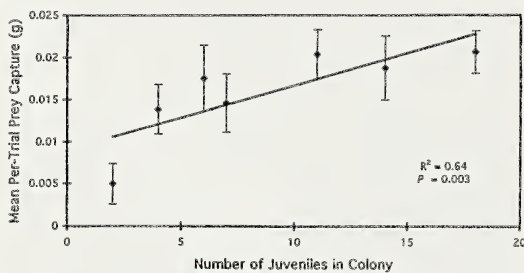


Figure 2.—Average per trial prey capture during the period juveniles were in the web vs number of juveniles in the colony. Plotted are the means for each colony over all instars with standard error bars ($R^2 = 0.64$, $P = 0.003$).

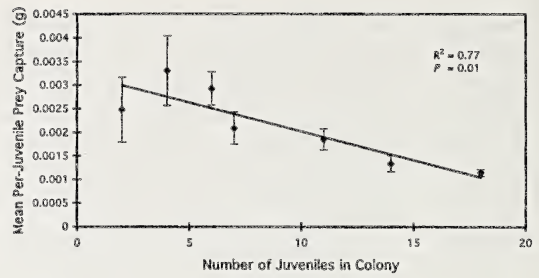


Figure 3.—Average per-juvenile, per-trial, prey capture during the period juveniles were in the web vs number of juveniles in the web. Plotted are the means for each colony over all instars with standard error bars ($R^2 = 0.77$, $P = 0.01$).

sixth instars, was not related to prey capture per juvenile (Fig. 6). Similarly, when these development rates were compared to the coefficients of variation in per-juvenile prey capture success, no trends were found (Fig. 7).

Experimentally dispersed fifth instar singletons captured fewer prey, on average, than the per-juvenile rate for a colony (Mann-Whitney $U = 56.0$, $P < 0.01$; Fig. 8A). The main cause of this difference was the fact that the singletons captured only *Drosophila* while the colonies were able to capture houseflies. The difference in prey capture did not result in a difference in development rate, as measured by the duration of the fifth instar, between colony juveniles and singletons (Mann-Whitney $U = 37.0$, $P = 0.92$; Fig. 8C). Male singletons captured significantly less prey (Mann-Whitney $U = 114.5$, $P = 0.002$), and developed significantly more slowly in the fifth instar

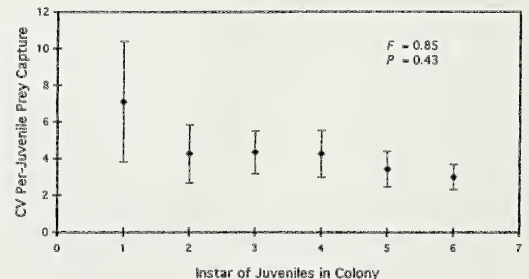


Figure 4.—Coefficient of variation in per-juvenile prey capture within instar, within colonies, vs stage of the colony. Plotted are the mean variances of the colonies at each instar with standard error bars (repeated measures ANCOVA $F = 0.85$, $P = 0.81$).

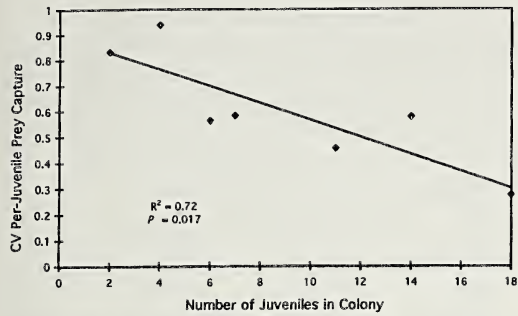


Figure 5.—Coefficient of variation in per-juvenile prey capture, within colonies, vs number of juveniles in the colony. Plotted are the variances for each colony pooled over all instars ($R^2 = 0.72$, $P = 0.017$).

(Mann-Whitney $U = 49.0$, $P = 0.002$), than female singletons (Figs. 8B, 8D).

Effects of delayed dispersal on a mother's future reproductive success.—To examine potential foraging benefits to the mother associated with delayed dispersal of her offspring, we compared prey capture within and among the webs of females which did not produce egg cases (Group A, Table 1), webs in which females were guarding egg cases that did not hatch (Group B, Table 1), and the webs from which the juveniles had been experimentally dispersed (Group C, Table 1). There were no differences in prey capture in the first week between any of the categories of webs, nor were the webs in which there were no juveniles more productive in the 5th week than they were at the first. Females who had had juveniles in their webs captured significantly more prey during the week after their offspring were dispersed (which on average was around the fourth week after being placed on the plant) than did either of the two categories that had not had juveniles. Prey capture of females the week after their juveniles were removed was not different than that of the week prior while the juveniles were still present.

DISCUSSION

The results presented here demonstrate that the presence of juveniles increased the overall productivity of webs, and that productivity increases with both the age (Fig. 1) and the number of juveniles in the web (Fig. 2). The majority of these effects were driven by the ability of larger and older colonies to capture

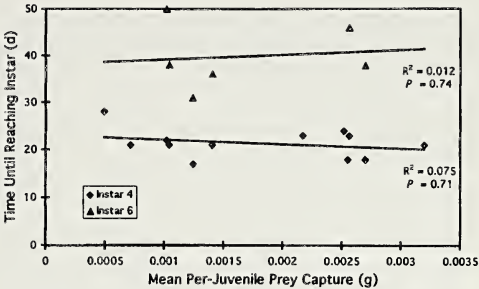


Figure 6.—Colonial juvenile development vs mean per-juvenile prey capture. The points plotted are the times taken by colonies to reach the specified instar (4th instar, $R^2 = 0.012$, $P = 0.74$; 6th instar $R^2 = 0.075$, $P = 0.71$).

more houseflies, one of which has more extractable resources than all ten of the *Drosophila* combined. These results are consistent with those found for several permanent-social spider species (Riechert et al. 1986; Tietjen 1986) including a congener of this species, *A. eximius* (Nentwig 1985; Rypstra 1990), as well as in colonial orb-weaving spiders (Uetz 1989). In these studies, social spiders captured larger prey and a wider range of prey sizes than solitary spiders of similar size.

There was a significant decrease in the coefficient of variation in per-juvenile prey capture associated with the number of juveniles in the colony (Fig. 5). Reduced variance in foraging success has been identified as a potential benefit of spider coloniality in a dynamic model (Caraco et al. 1995), and in colonial orb-weaving *Metetepeira* spp. (Uetz 1988a, 1988b). These studies found that, under high prey densities, coloniality represents

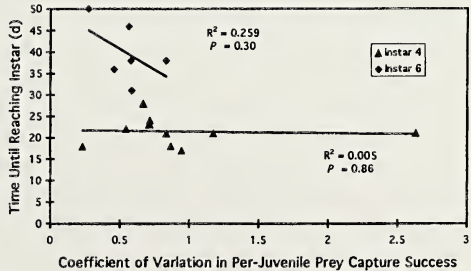


Figure 7.—Colonial juvenile development vs mean coefficient of variation in per-juvenile prey capture. The points plotted are the times taken by colonies to reach the specified instar (4th instar, $R^2 = 0.259$, $P = 0.30$; 6th instar $R^2 = 0.005$, $P = 0.86$).

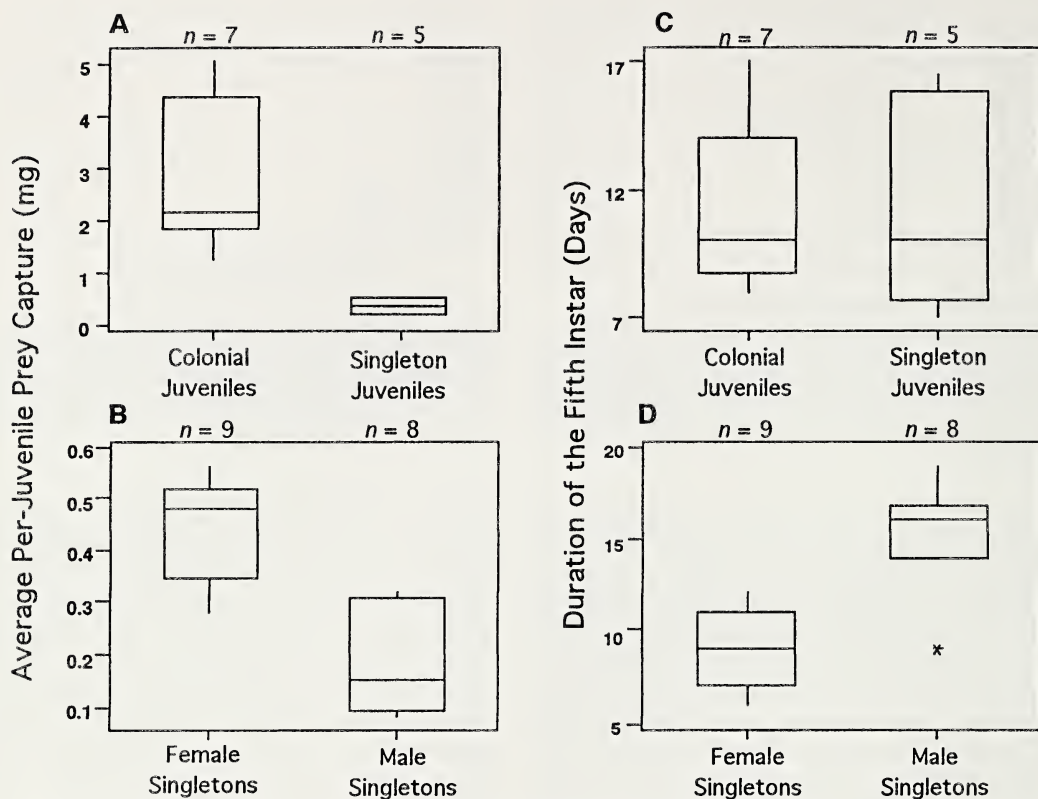


Figure 8.—Boxplots comparing prey capture and juvenile development between colonial and singleton juveniles. Plotted are the medians, inter-quartile ranges and standard ranges (see text for significance statistics).

a 'risk averse' strategy in which the spiders trade a reduction in mean individual capture rate for a reduction in variance in capture rate.

We found no relationships between mean or CV in per-juvenile prey capture and development rate (Figs. 6, 7), nor did the singleton juveniles develop more slowly than colonial individuals, despite the greatly-reduced prey capture in singletons (Fig. 8C). This suggests that, under these prey densities, the colonies were capturing considerably more prey than they could physiologically assimilate.

Female singletons were more successful at capturing prey than male singletons (Fig. 9B). Though not measured directly, the female singletons' webs appeared larger and denser than those of the males. Among the non-territorial permanently-social spiders, males typically do not participate in web activities, and in such species the adult sex ratios are skewed towards females (Avilés 1997). These skewed sex ratios have apparently evolved through

group selection, meeting the stringent conditions required to select for a trait which is beneficial to the colony but which, within the colony, reduces the fitness of individuals possessing it (Avilés 1986, 1993; Smith & Hagen 1996). The data presented here suggest that female *A. studiosus* may benefit by skewing their broods toward females. If web productivity increases with the proportion of female juveniles, there may be an optimal brood sex ratio which balances the increased survivorship of female-biased broods, with Fisher's (1958) selective pressure towards an equal investment between male and female offspring. A female biased sex ratio was reported for this species in a Tennessee population (Furey 1998), but was not found among specimens from Ecuador (Avilés & Maddison 1991).

The results presented here suggest that *A. studiosus* juveniles benefit from remaining in their natal web by obtaining more resources, and more consistent resources, than they

Table 1.—Weekly web productivity averages, variances and specific comparisons (*T* statistics and *P* values) for three types of web. Group A females did not produce egg sacs, Group B females produced egg cases which did not hatch, and Group C females produced egg cases which hatched, and had their juveniles removed at the fourth instar.

Week	Group A No egg sac produced (<i>n</i> = 8)		Group B Eggs did not hatch (<i>n</i> = 6)		Group C Juveniles removed at 4th instar (<i>n</i> = 5)		
	Wk 1	Wk 5	Wk 1	Wk 5	Wk 1	Wk 4	Wk 5
Mean (g)	0.0017	0.0033	0.0014	0.0034	0.0032	0.0156	0.0150
Variance	3.6 E-6	4.0 E-6	4.5 E-6	6.1 E-6	1.2 E-5	1.3 E-5	5.4 E-5
A (wk 1)	—	-1.63 <i>P</i> = 0.073	0.26 <i>P</i> = 0.40		-1.04 <i>P</i> = 0.16		
A (wk 5)		—		-0.021 <i>P</i> = 0.49			-8.0 <i>P</i> = 3 E-6
B (wk 1)			—	-1.28 <i>P</i> = 0.13	-1.07 <i>P</i> = 0.156		
B (wk 5)				—			-6.69 <i>P</i> = 5 E-5
C (wk 1)					—		-10.2 <i>P</i> = 0.0003
C (wk 4)						—	-0.18 <i>P</i> = 0.43
C (wk 5)							—

would as singletons. However, because per-individual prey capture decreases with colony size (Fig. 3), for any given prey density there will be an upper limit to the number of juveniles a colony can support. Colony sizes in this experiment were lower than those reported for natural colonies (a mean of 36 juveniles at hatching; Brach (1977)).

While the potential benefits of delayed dispersal to the juveniles are relatively clear, there is indirect evidence that there are benefits to the mother as well. In this study, females in webs that previously had juveniles captured more prey than those with webs of the same age that had not (Table 1), but webs that had had juveniles were no less productive during the week after the juveniles were removed than during the previous week with the juveniles present. This suggests that the juveniles' main contribution to web productivity is in web construction rather than in subduing prey. While size of webs was not measured, webs with juveniles present became noticeably larger than webs without.

Because there is no observed aggression between a mother and her younger offspring, or among juveniles (Brach 1977), it is likely that captured prey is divided evenly (or at

least randomly) among colony members. Observations of interactions among colony members are limited for this species, and it is possible for the mother or larger juveniles to dominate captured prey. Further work is needed to explore potential sibling rivalries and parent-offspring conflicts in this species.

It should be kept in mind that, in this experiment, prey densities were artificial, standardized, and depletable. Prey densities were chosen in an attempt to eliminate nutritionally related mortality, not to represent natural conditions. Therefore, the extent to which the protocol reflects conditions associated with the evolutionary maintenance of *A. studiosus* behavior is limited; however, the internal comparisons of the experiment remain robust. The depletion of the prey in a given trial puts an upper limit on possible prey capture success (although in only two trials did a web capture all of the prey released). Prey density during a trial decreased as prey were captured, resulting in a decline in the probability of capturing more prey. Overall, prey depletion should have the effect of reducing the power of the experiment to detect factors that affect the mean capture rate of webs; prey depletion may also create a spurious reduction in vari-

ance measures as the more productive webs approach prey depletion.

That neither colonial nor singleton juveniles appeared to be food-limited in this study is suggested by the stable growth rates of juveniles regardless of group size or prey capture rate. These results would predict that under lower prey densities food limitation would affect the singleton juveniles more than colonials, except when the colony is so large that the per-juvenile prey capture is below that of singletons. As long as prey densities are high enough on average to support the colonies, the reduction in variance associated with cooperative foraging may allow the juveniles to assimilate the resources more efficiently.

The data presented here suggest that delayed dispersal of a brood could enhance the mother's production of future broods by increasing the productivity of her web. The experimental conditions were relatively mild, compared to natural conditions where webs are frequently damaged, particularly by rainfall. Thus, cooperative web maintenance in this species may be even more important than this study would suggest.

From these experimental data, it seems likely that cooperative foraging plays a significant role in the evolutionary maintenance of delayed offspring dispersal in *Anelosimus studiosus*. While this work has identified several potential advantages of delayed dispersal, the specific nature of the costs and benefits would need to be tested under more natural conditions. This is also true for other factors which could influence the maintenance of delayed dispersal such as predation risk and parasitism.

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RESOURCE PARTITIONING OF SPIDER HOSTS (ARACHNIDA, ARANEAE) BY TWO MANTISPID SPECIES (NEUROPTERA, MANTISPIDAE) IN AN ILLINOIS WOODLAND

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ABSTRACT. Two spider-boarding mantispids, *Mantispa uhleri* Banks 1943 and *Climaciella brunnea* (Say 1824), were found to be partitioning available spider egg resources in an Illinois woods based on vertical stratification. *Mantispa uhleri* was found to be phoretic on the philodromid *Philodromus vulgaris* (Hentz 1847), the salticid *Metacyrba undata* (De Geer 1867) and the anyphaenid *Aysha gracilis* (Hentz 1847) at levels of 75%, 26%, and 27% respectively. All of these spiders were collected from areas above the forest floor. In contrast, *C. brunnea* was collected from 19% of leaf litter-inhabiting lycosids of the genus *Schizocosa*. There was no host range overlap within the woods, but in a grassy field without appreciable stratification of vegetation adjacent to the woods, both *M. uhleri* and *C. brunnea* were found aboard the lycosid *Rabidosia punctulata* (Walckenaer 1837) at levels of 2% and 7% respectively. A single larva of *Mantispa pulchella* (Banks 1912) associated with an anyphaenid from the woodland sample was also collected in this study. Mantispids are far more common than has been previously supposed and are likely an important factor in spider population dynamics and the evolution of spider behavior.

Keywords: *Mantispa uhleri*, *Climaciella brunnea*, *Mantispa pulchella*

The neuropteran family Mantispidae, subfamily Mantispininae, contains insects whose larvae are spider-egg predators (Redborg 1998). Larvae obtain eggs in one of two ways: (1) direct penetration of an egg sac by first instar larvae that search for egg sacs in the field, or (2) boarding adult female spiders and entering the spider's egg sac while it is being constructed (Redborg & MacLeod 1985). Inside the egg sac, larvae pierce and drain the eggs with a sucking tube formed by modified mandibles and maxillae. After three larval instars, the developing mantispid spins a cocoon inside the egg sac using silk from the Malpighian tubules.

The species of spiders utilized by mantispids in North America are partially known for a number of species including *Mantispa uhleri* Banks 1943 (Redborg & MacLeod 1985), *Mantispa fuscicornis* Banks 1912 from Texas (Rice 1986; Rice & Peck 1991, cited as *Mantispa sayi* Banks 1897) and *Mantispa pulchella* (Banks 1912) (Hoffman & Brushwein 1989), *Mantispa interrupta* Say 1825 (Hoffman & Brushwein 1990) and *Mantispa viridis* Walker 1853 (Brushwein et al. 1992) from South Carolina. Much of this work has not been quantitative. Moreover, little is known

about how sympatric mantispids interact in their selection of hosts. Here we report on the resource use of two mantispid species in Illinois.

The present study developed while we were collecting overwintering larvae of *M. uhleri* for a laboratory experiment from two of its host spiders, *Philodromus vulgaris* (Hentz 1847) (Philodromidae) and *Metacyrba undata* (De Geer 1867) (Salticidae) in a small woodland, and discovered unexpectedly high levels of infestation. In the spring we collected other types of spiders for comparison and discovered a second species of mantispid, *Climaciella brunnea* (Say 1824), aboard many of them. Because until that time no data had yet been reported documenting more than one mantispid species from the same study site, we continued our collections to see if there was any pattern to the kinds of spiders boarded. It became apparent that these two mantispids were not boarding the same species of spiders.

METHODS

Mantispids are associated primarily with hunting spiders (Redborg & MacLeod 1985; Hoffman & Brushwein 1989, 1990; Redborg 1998). We collected cursorial spiders from

four microhabitats in a four-hectare, oak-hickory forest near Mahomet, Illinois known as Stidham Woods.

Spiders were collected from (1) beneath tree bark during the winter, (2) on shrub-level foliage during the early spring, (3) from the woodland leaf litter during the late spring, summer, and early fall, and (4) from grassy fields bordering the woods during the late summer and early fall. Spiders were later anesthetized with CO₂ and examined under a stereo microscope at 18× magnification for the presence of mantispid larvae. Mantispid boarding frequencies on spiders were analyzed using Chi-square or the Fisher Exact Test.

Bark-associated spiders.—Spiders were collected from beneath the bark of eight living shagbark hickories, *Carya ovata* K. Koch, distributed throughout the entire woods, between 18 December 1982 and 5 February 1983. Loose bark was removed from the trunk up to a height of 4 m. A white sheet was placed around the base of each tree to catch any spiders that fell from the bark.

Between 12 June 1983 and 22 June 1983 additional shagbark hickories were examined for the presence of female spiders guarding egg sacs. Bark was pulled back and the undersurface of it examined. Egg sacs and associated spiders were collected, brought into the laboratory, and the presence of mantispid cocoons and emergence of any adult mantispids were recorded.

Low-level foliage spiders.—Spiders were located on the branches of small trees and shrubs with the aid of a headlamp and collected by hand on 16 May 1983, 19 May 1983 and 21 May 1983.

Leaf litter lycosids.—Wolf spiders (Lycosidae) were collected by hand on three nights in late spring between 21–28 May 1983 from the leaf litter within the woods at night aided by eye reflections from a headlamp. A second sample was taken in mid summer on 30 June. A third sample was taken in the fall on 19 & 26 September 1983.

Egg sacs were obtained from, or collected with, some of these spiders. Spiders and egg sacs were maintained under ambient temperature and photoperiod on a screened porch.

Field lycosids.—Wolf spiders were collected from the grassy field to the north of the woods using a headlamp as described above

on seven nights between 3 August–26 September 1983.

Adult *Climaciella* observations.—Since *Climaciella* adults are known to frequent flowers, the field area to the east and north of the woods was surveyed approximately once a week from 1 July 1983 to 4 September 1983 for the presence of *Climaciella* adults on flowers. This time frame was chosen based on our collection of *Schizocosa* adults with egg sacs in late June (see results).

Voucher specimens of this study are deposited in the Field Museum of Natural History.

RESULTS

Bark-associated spiders.—Most of the spiders collected belonged to two species, *Philodromus vulgaris* and *Metacryba undata* (Table 1). *Philodromus* sits loose beneath the bark and does not produce any type of silken retreat. Some of these spiders were concealed in cracks or crevices while others, aided by their flattened morphology, simply sat adhered to the under surface of the outer bark or the outer surface of the inner layers. Many spiders fell from the tree when the bark was removed and were recovered from the sheet. Specimens of *M. undata* were all contained within dense silken retreats. *Cheiracanthium mildei* (Clubionidae), *Ariadna bicolor* (Segestriidae) and *Herpyllus ecclisiastica* (Gnaphosidae) occupied silk retreats less dense than those of *M. undata*.

Spiders carrying mantispid larvae were collected from all eight trees examined. A high frequency of 64 out of 85 *P. vulgaris* (29 subadult ♀, 30 subadult ♂, 5 juveniles) had been boarded by at least one larva of *M. uhleri*. Eight of these spiders carried more than one larva (seven with two, one with three), most of which (68 out of 73) were tightly adhered to the dorsal, ventral, or lateral surface of the pedicel. Although larvae will enter the book lungs of sufficiently large species of spiders (Redborg & MacLeod 1985), none were found in this area on *Philodromus*. The remaining larvae were located at various positions around the leg bases or underneath the edge of the carapace.

Mantispa uhleri larvae were also found aboard the salticid *Metacryba undata* although its infestation frequency of 25 out of 85 (26%) was significantly lower ($\chi^2 = 43.19$, $P < 0.001$) than the frequency of 64 out of 98

Table 1.—Collections of cursorial spiders from four microhabitats in Stidham Woods, Illinois during 1982–83. (* = May collection; ** = June collection; *** = September collection.)

Micro-habitat	Species	No. of					Total
		No. of juven-iles	No. of adult fe-males	No. of sub-adult males	No. of adult fe-males	No. of adult males	
bark	<i>Philodromus vulgaris</i> (Hentz 1847)	9	36	40			85
bark	<i>Metacyrba undata</i> (De Geer 1867)	68			18	12	98
bark	<i>Cheiracanthium mildei</i> C. L. Koch 1864	1	1				2
bark	<i>Ariadna bicolor</i> (Hentz 1842)	10					10
bark	<i>Herpyllus ecclisiastica</i> Hentz 1832	6					6
foliage	<i>Aysha gracilis</i> (Hentz 1847)	1			6	4	11
foliage	<i>Anyphaena fraterna</i> (Banks 1896)	1			19	18	38
litter*	<i>Schizocosa saltatrix</i> (Hentz 1844)				1		1
litter*	<i>Schizocosa ocreata</i> (Hentz 1844)				4	6	10
litter*	<i>Schizocosa rovneri</i> Uetz and Dondale 1979				1		1
litter*	<i>Schizocosa</i> sp.		55	53			108
litter**	<i>Schizocosa saltatrix</i>				1		1
litter**	<i>Schizocosa ocreata</i>					1	1
litter**	<i>Schizocosa ocreata/rovneri</i>				12		12
litter**	<i>Schizocosa</i> sp.		4				4
litter***	<i>Schizocosa</i> sp.	40					40
field	<i>Rabidosa punctulata</i> (Hentz 1844)	38	19	23	59	46	185
field	<i>Rabidosa rabida</i> (Walckenaer 1837)				5	1	6
field	<i>Hogna carolinensis</i> (Walckenaer 1837)	2					2

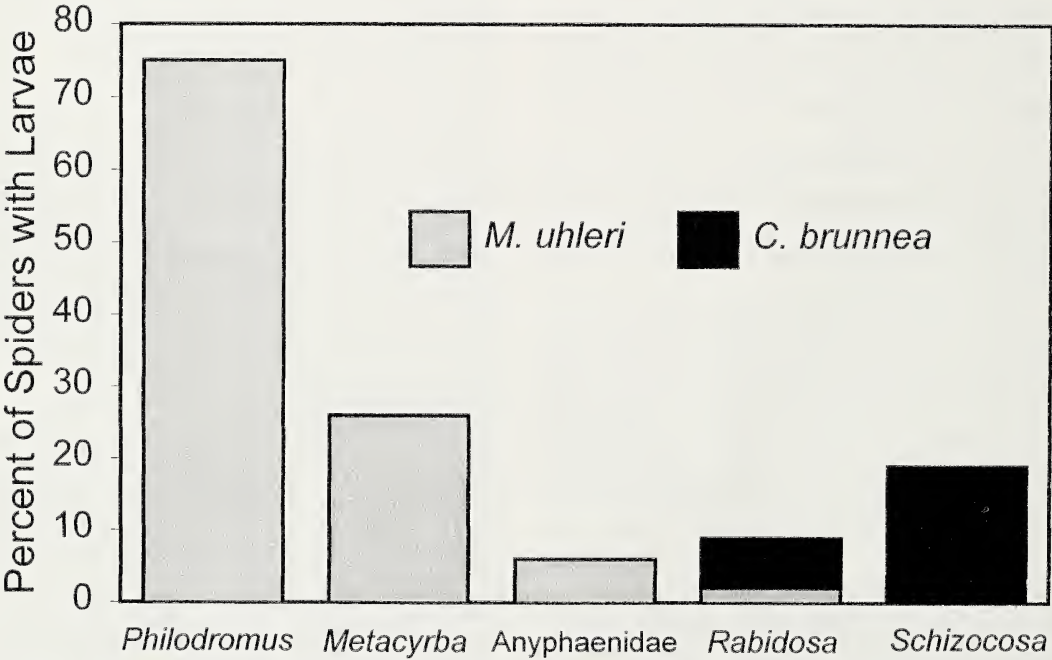


Figure 1.—Percentages of five groups of spiders boarded by first instar larvae of *Mantispa uhleri* and *Climaciella brunnea* (Neuroptera: Mantispidae) from an Illinois woodland. Collections of *Aysha gracilis* and *Anyphaena fraterna* were pooled and are designated Anyphaenidae.

(75%) on *P. vulgaris*. Twenty-five *M. undata* (5 adult ♀, 6 adult ♂, 14 juveniles) had been boarded by at least one larva of the mantispid and two of these spiders carried two larvae each. Most larvae were located on the dorsal, ventral, or lateral pedicel while no larvae occupied the book lungs. One additional bark-associated spider was found boarded by a larva of *M. uhleri*. A subadult female *Cheiracanthium mildei* carried a larva in the right book lung.

***Philodromus* egg sac collections.**—Five female *P. vulgaris* guarding egg sacs were collected on 12 June 1983, 13 were collected on 16 June 1983, and eight were collected on 22 June 1983 for a total of 26 spiders. With the exception of one spider collected on 12 June, all spiders were guarding two egg sacs. In all cases, egg sacs were located on the inner surface of the removed piece of bark. The two sacs were close enough together so that the legs of the spider came in contact with both. The sequence of the two sacs was easy to determine by the differing developmental state of the eggs within and the second egg sac constructed was always the smaller of the two.

Eight of the 26 spiders were guarding sacs that contained a larva or cocoon of *M. uhleri*. The egg sac attacked was always the larger, first sac. Adult mantispids emerged from these sacs on 29 June, 30 June (4 mantispids), 2 July (2 mantispids), and 3 July 1983. Six of the spiders also had egg sacs containing wasp larvae, although which sac was involved varied. One or more wasps emerged from four of the older, first sacs. Wasps were in both of one spider's egg sacs, and one spider that had a mantispid in its first sac had a wasp in the second. Although 75% of overwintering *P. vulgaris* had been boarded by *M. uhleri* larvae, only 31% of the spring egg sacs contained larvae. The frequencies associated with these two percentages are significantly different ($\chi^2 = 15.4$, $P < 0.001$).

Low-level foliage spiders.—All of the spiders collected from this microhabitat were anyphaenids belonging to two species (Table 1). The overall infestation level of *M. uhleri* on Anyphaenids was 6% (3 out of 49). Three *A. gracilis* (1 ♀, 2 ♂) out of 11 carried a larva of *M. uhleri* with two of these larvae on the pedicel and one in a book lung. No larvae were found aboard the 38 *A. fraterna*. The frequencies of *M. uhleri* on these two anyphaenid spe-

cies were significantly different (Fisher Exact Test, $P = 0.009$). The infestation frequency of 3 out of 11 (27%) on *A. gracilis*, however, was no different ($\chi^2 = 0.06$, $P > 0.05$) from that on *M. undata* but was significantly less ($\chi^2 = 8.50$, $P < 0.01$) than that on *P. vulgaris*.

A single larva of *M. pulchella* was also found associated with one of these anyphaenids. It unfortunately was dislodged from its host spider and found loose in the examination chamber with representatives of both spider species so that its exact host association could not be determined.

Leaf litter lycosids.—A total of 120 spiders was collected in May with a second smaller sample of 18 spiders collected in late June (Table 1). Only adult spiders could be reliably identified to species. *Schizocosa ocreata* and *S. rovneri* are sibling species whose males can easily be distinguished by the tufts of black bristles on leg 1 of *S. ocreata* but whose females are morphologically identical (Uetz & Dondale 1979). Some of these females were reliably identified by successfully mating them with a male of the appropriate species. If adult females could not be so mated, they are referred to as *S. ocreata/rovneri* as they could have been either species.

Twenty-three of the 120 (19%) spiders (3 ♀ *S. ocreata*, 1 ♂ *S. ocreata*, 11 subadult ♀ *Schizocosa* sp., 8 subadult ♂ *Schizocosa* sp.) collected at the end of May 1983 had been boarded by at least one larva of *C. brunnea*. Two of these spiders (1 ♀ *S. ocreata* and 1 subadult ♀ *Schizocosa* sp.) carried two larvae. Unlike larvae of *M. uhleri*, which are usually tightly adhered to the pedicel, these larvae were located along the edge of the carapace with their heads oriented toward the pedicel or toward the membranous area between the edge of the carapace and the coxae. Larvae of *M. uhleri* show no visible movement while attached to the pedicel, but larvae of *Climaciella* could be seen to periodically move along the carapace and they could often be seen to seemingly push their mouthparts into the soft areas beneath it. Small drops of what appeared to be spider hemolymph could sometimes be seen adjacent to larval mouthparts or in areas where larvae had recently been.

Of the 18 spiders collected late June, four (2 ♀ *Schizocosa* sp., 2 subadult ♀ *Schizocosa* sp.) carried a larva of *C. brunnea*. One of the adult females produced an egg sac on 3 July

Table 2.—Levels of *Mantispa uhleri* and *Climaciella brunnea* (Mantispidae) aboard the spider *Rabidosa punctulata* (Lycosidae) collected from grassy fields north of Stidham Woods, Illinois in 1983 (* one spider boarded by both mantispid species).

Date	No. of spiders				No. of mantispids	
	Juveniles	Subadults	Adults	Total	<i>M. uhleri</i>	<i>C. brunnea</i>
Aug. 3, 4	34	0	0	34	1*	1*
Aug. 18	2	38	0	40	2	4
Aug. 31	1	4	35	40	1	3
Sept. 19, 21	1	0	32	33	0	2
Sept. 26	0	0	38	38	0	3
Total	38	42	105	185	4	13

1983. On 23 July 1983 an adult male *C. brunnea* emerged from this sac. Three of the adult female spiders not carrying a mantispid larva had an egg sac when collected. Spiderlings emerged from these egg sacs on 7 July, 11 July, and 17 July 1983.

Seven of the 40 juvenile *Schizocosa* collected in September (Table 1), presumably the offspring from July egg sacs, carried a single larva of *C. brunnea*.

The three *Schizocosa* samples yielded no larvae of *M. uhleri*. The frequencies of *Climaciella* infestation were 19%, 22%, and 18%, respectively. They were not significantly different ($\chi^2 = 0.18$, $P > 0.05$) from each other.

Field lycosids.—Collections were predominated by *Rabidosa punctulata* (Table 1). This species overwinters as an adult and produces egg sacs in the spring. Consistent with this scenario, juveniles were collected in early August, subadults in mid-August, and adults in late August and September.

In contrast to the other spiders in this study, *R. punctulata* was boarded by larvae of both *M. uhleri* and *C. brunnea* (Table 2). In fact, one of these spiders carried a larva of both mantispid species. All of the other boarded spiders carried only a single larva. Of the 185 *R. punctulata* collected, four (2%) had been boarded by *M. uhleri* while 13 (7%) had been boarded by *C. brunnea*. Although the frequency of *C. brunnea* on *R. punctulata* was significantly greater than that of *M. uhleri* ($\chi^2 = 3.95$, $P < 0.05$), there were significantly more *C. brunnea* on *Schizocosa* in May ($\chi^2 = 9.17$, $P < 0.005$). No mantispids were found on either *R. rabida* or *H. carolinensis*.

Adult *Climaciella* collections.—The fields

to the north and west of the woods were surveyed for adult mantispids on flowering plants approximately weekly on 10 dates in July, August and September. In July, the most conspicuous plants in bloom included red clover, *Trifolium pratense* L.; wild carrot, *Daucus carota* L.; ox-eye daisy, *Chrysanthemum leucanthemum* L.; and common milkweed, *Asclepias syriaca* L. These were followed in August by thistle, *Cirsium* spp. and sunflower, *Helianthus* spp. and, in September, goldenrod, *Solidago* spp. The only mantispids found on these plants were five *C. brunnea*. Three females were observed on three different milkweed plants on 17 July. A courting male was found associated with one of these females. The male's behavior was similar to that described by Boyden (1983) for *C. brunnea* on milkweed in Minnesota. A sweet musk-like odor, presumably pheromone, from this male was quite apparent. A fourth female was observed, also on milkweed, a week later on 23 July.

DISCUSSION

It was actually more difficult to find a specimen of *P. vulgaris* from Stidham Woods not carrying a mantispid than it was to find one that did. While the exceedingly high levels of both *M. uhleri* and *C. brunnea* at this field site may seem excessive to some, we contend this is not an anomaly. An ongoing study of the distribution of mantispids in Iowa has so far involved the collection of over 5000 specimens of *P. vulgaris* and *M. undata* and, in areas in eastern Iowa where *M. uhleri* occurs, its levels on *P. vulgaris* range from 16–70% and on *M. undata* range from 8–33% (unpubl. data). Thus, while the levels of 75% and 26%

reported here are high, they are not incongruous and certainly comparable to levels found in Iowa. Scheffer (1992) recently reported associations between *Climaciella* and *Schizocosa* from Cincinnati and northern Kentucky. Although she did not report frequencies, her report does not suggest that spiders bearing *Climaciella* larvae were difficult to find.

Up to now, most mantispid studies have dealt with single species and have focused primarily on the documentation of spider hosts. Data are now needed involving sympatric species of mantispids collected from an area small enough to make some meaningful comparisons regarding resource partitioning. A recent study reports two Japanese mantispids boarding two different groups of spiders in deciduous forests (Hirata et al. 1995). Larvae of *Mantispa japonica* were found on spiders collected on plants while *Eumantispa harmandi* were found aboard spiders associated with the forest floor. However, no levels of infestation were reported and no statistical comparisons made.

Both *M. uhleri* and *C. brunnea* are spider boarders that overwinter on their respective host spiders and enter egg sacs when they are constructed the following year. Although *M. uhleri* will board a wide variety of hunting spiders, it is becoming increasingly apparent that *P. vulgaris* is its major host in much of the North American Midwest. Larvae of *M. uhleri* enter *P. vulgaris* egg sacs in May and June and emerge as adults in late June and early July. Newly-hatched *M. uhleri* larvae should begin appearing in mid-to-late July.

While the spider *M. undata* is also an important host for *M. uhleri*, its role pales in comparison to that of *P. vulgaris*. Hoffman & Brushwein (1989) hypothesized that *M. pulchella*'s greater association with anyphaenids, salticids, and clubionids as opposed to philodromids, oxyopids, and thomisids was due to the fact that the former spiders make silken retreats that perhaps enabled larvae to locate or board them more easily. There is no evidence for this in *M. uhleri* because *P. vulgaris* lacks retreats. Also, the flattened resting posture of *Philodromus* would allow much leg and venter surface area to contact the substrate, thus facilitating larval contact.

Both spider groups reported here (*Schizocosa* and *Rabidosia*) as hosts for *C. brunnea* are the same as those reported by Redborg &

MacLeod (1983) in southern Illinois. Of the two host groups, the most important appears to be members of the genus *Schizocosa*. The infestation level of 19% on the nearly mature *Schizocosa* collected in May represents larvae that likely had overwintered on these spiders. Our collecting data suggest that egg sacs from *Schizocosa* probably are produced in late June and early July. The emergence of the *C. brunnea* adult on 23 July from the egg sac of a *Schizocosa* collected 30 June corresponds with the appearance of adults on milkweed in the field. One might therefore expect newly-hatched *Climaciella* larvae to begin appearing in late July or early August. These would be the larvae that were then found on the juvenile *Schizocosa* in September. The almost identical level of 18% infestation on these spiders compared to those collected in May suggests that *Climaciella* population levels were fairly stable.

Within the wooded area, there was absolutely no overlap of host range between *M. uhleri* and *C. brunnea*. The division of spider resources seems to be based on vertical stratification. All of the spiders associated with *M. uhleri* are foliage-inhabiting spiders while the main host for *C. brunnea*, *Schizocosa*, is usually confined to the forest floor. One could argue that this differential association is due to restricted host preferences on the part of the larvae, but we think it more likely due to differences in adult ovipositional or larval searching behavior. *Mantispa uhleri* will readily board lycosids under laboratory conditions and has been found at various times on virtually every group of hunting spiders including species of *Schizocosa* in southern Illinois (Redborg & MacLeod 1985), and *Climaciella* will board spiders other than lycosids in the laboratory (Redborg & MacLeod 1983). While it is true that all of the associations in this report, as well as all other published data, link *Climaciella* with lycosids, we think this can best be explained by behavioral factors which keep *Climaciella* larvae close to the ground.

Although there is currently no direct evidence documenting ovipositional sites for *M. uhleri* in the field, its high levels on *Philodromus* suggest that this mantispid may be laying its eggs in the foliage or branches of the forest canopy. Our observations through the years suggest to us that *P. vulgaris* develops

in the tree canopy. For instance, each October, following the first frost, appreciable numbers of subadult *Philodromus* can be found collecting between the window frames and sills of the science building on the Coe College campus. These spiders are not evident during the summer on the walls of the building and there is no significant low-lying vegetation surrounding the building other than the frequently-mowed lawn. It seems reasonable that the spiders have been developing on the foliage or branches of the several oaks that line the grounds around the building. We regard the window sills and frames of the building as being the "urban" ecological equivalent of loose bark. Published data concerning the life history of this spider are crucially needed.

In contrast, we suggest that *C. brunnea* adults, although they may aggregate, mate and feed on nearby flowers, enter the woods and lay their eggs on or near the ground. *Climaciella* larvae do not actively search as do the larvae of *M. uhleri* but instead adopt a phoretic posture in which they rear up on their tails and sway back and forth with legs outstretched (Redborg & MacLeod 1983). It is thus not likely that larvae will travel a great distance from their egg clutch. Their strategy as obligate spider boarders is to wait for spiders to come to them. They would be most likely to come in contact with active spiders which certainly characterizes the Lycosidae. To produce infestation levels of 19% on *Schizocosa*, that waiting place, and by extension the site of adult oviposition, is most probably on or near the ground.

In light of these arguments, the occurrence of larvae of both species of mantispids on *R. punctulata* in the field adjacent to the woods is corroborative. The vegetation here has limited vertical stratification of no more than a few feet. Mantispids of either species that attempted to oviposit in the field would wind up laying eggs in basically the same area—on the ground, on various grasses, or on the foliage of low-lying plants. The salt marsh in southern Mississippi studied by LaSalle (1986) would have been structurally somewhat reminiscent of the area studied here. He found *Climaciella* there laying eggs at the tips of leaf spikes of *Juncus* rushes. We can imagine similar ovipositional behavior here for both *M. uhleri* and *C. brunnea*. *Rabidosa punctulata*, along with its sibling species *R. rabida*,

is usually found in grassy areas. Spiders were collected both on the ground and crawling along the foliage of grasses and other plants. Thus, whatever vertical stratification is present is probably completely traversed by this spider. And this, appropriately enough, is the one place where there is overlap of host range. We found larvae of both species on this spider. In fact, one spider carried a larva of both *M. uhleri* and *C. brunnea*. This is, to our knowledge, the first documentation of two different species of mantispid aboard the same spider.

It is important to note that the 2% infestation level of *M. uhleri* and the 7% level of *C. brunnea* on *R. punctulata* are both significantly lower than their respective levels on other spiders, suggesting that the field area is not the preferred ovipositional location for either species. Also strongly supported is the contention that *C. brunnea* is leaving its flower-inhabiting aggregation areas to lay its eggs within the woods. If adults were preferentially laying their eggs near their mating sites on milkweed, one would expect to find significantly more larvae on *R. punctulata* than *Schizocosa*. Just the opposite is true. The significantly higher level of *C. brunnea* on *R. punctulata* compared to that of *M. uhleri* is consistent with the sit-and-wait specialization of this mantispid that may favor the selection of lycosids as hosts. Although neither parasite favored the grassy field area for oviposition, *C. brunnea* may wind up laying more eggs there because of the necessity to travel between the two sites.

While the infestation level of *M. uhleri* on *R. punctulata* is slight, the infestation level of *C. brunnea* on this spider is more substantial. There is the potential for a complex, overlapping life cycle similar to those described for *M. uhleri* (Redborg & MacLeod 1985) and *M. pulchella* (Hoffman & Brushwein 1989). *Rabidosa punctulata* females overwinter as adults and produce egg sacs early in the spring. Larvae that survived the winter on this spider would probably have emerged from egg sacs before we looked for adults in the summer. *Climaciella* offspring might appear early enough in the year to board *Schizocosa* spiders destined to spin egg sacs that same summer, or they might board immature *R. punctulata* that would not spin sacs until the following year. One or two generations per year are thus possible. Future study will be

necessary to assess the importance of this spider in the population dynamics of *C. brunnea* and vice-versa.

The finding of a single larva of *M. pulchella* on one of the anyphaenids in this study is intriguing. It is consistent with the findings of Hoffman & Brushwein (1989) who found *M. pulchella* in South Carolina associated with small foliage-inhabiting wandering spiders. In fact, anyphaenids yielded the greatest number of *M. pulchella* larvae in their study with both *A. fraterna* and *A. gracilis* serving as hosts. More extensive collecting of small wandering spiders might have uncovered additional larvae of *M. pulchella* and the existence of a third level of resource partitioning in Stidham Woods. It is also possible that *M. pulchella* is truly rare here, perhaps unable to compete successfully on its normal hosts due to the high level of competition from *M. uhleri*.

If one focuses on the anyphaenids as a group, the infestation level of *M. uhleri* is only 6%, intermediate between the high levels on *Philodromus/Metacryba* and the non-existent level on *Schizocosa*. However, this may be misleading. All *M. uhleri* associated with this family were aboard *A. gracilis* and none aboard *A. fraterna*. It is possible that these two spiders, although collected from the same microhabitat early in the spring, may be occupying different areas during the critical time when *M. uhleri* larvae are boarding them. Still, Redborg & MacLeod (1985) did find *M. uhleri* aboard *A. fraterna* in southern Illinois. More extensive sampling will be needed to answer this question.

While 75% of overwintering *P. vulgaris* had been boarded by *M. uhleri* larvae, only 8 of 26 (31%) of egg-laying *P. vulgaris* were affected with a larva in their first sac. This significant difference shows that some larval mortality occurs between overwintering and egg sac production. There may be spider behavioral mechanisms that reduce the number of larvae successfully entering egg sacs. Of particular interest here are the two egg sacs spun and guarded by this spider. Mantispid larvae were only found in the larger first egg sac. Eggs in the second egg sac escaped predation, at least by mantispids. This is very high selective pressure which could have shaped the egg-laying strategy of *P. vulgaris*. Recent evidence (Vittitoe 1991) indicates that

the second egg sac of *P. vulgaris* is an anti-mantispid mechanism evolved specifically to thwart *M. uhleri* predation.

The small area of our study site may have affected the way in which these two mantispids interacted here. Perhaps in larger more extensive woods, *C. brunnea* is restricted to the interface between woods and field while *M. uhleri* populations are more homogeneously distributed in woods or even concentrated within the interior. Such spatial differences might be muddled in small woodlands. Thus resource partitioning between these two species may involve additional horizontal components.

We acknowledge that our sample of hunting spiders from Stidham Woods deals with only a small number of species and is thus incomplete, but the four different microhabitats they represent provide a good beginning for understanding the differences between these two mantispids. Future work should focus on additional spider groups, particularly those of the surrounding fields, where greater overlap between *M. uhleri* and *C. brunnea* is predicted.

In 1975 we attended the annual meeting of the American Arachnological Society and one of us (K.E. Redborg) presented some preliminary graduate student research on spider boarding behavior by larval mantispids. Findings suggested that these insects were much more common than had been previously supposed. Following the talk B.J. Kaston commented that, although he found the results interesting, his general impression through the years was that mantispids were "as scarce as hen's teeth." Later, H.W. Levi informed us that he had commonly seen what appeared to be such larvae attached to the pedicel of spiders that he had collected in Wisconsin. A few weeks after the meeting J.E. Carrel wrote that, sparked by our discussions, he had examined a large container of preserved wolf spiders from his lab and discovered a "scum" of mantispid larvae floating on the top. Some textbooks still regard mantispids as being a novel but obscure group of insects, at least in temperate North America. The time has now arrived when these fascinating insects may no longer be regarded as rare but can more properly be assessed as having an important impact on spider ecology and an important role in the evolution of spider behavior.

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EFFECTS OF FERTILIZER ADDITION AND DEBRIS REMOVAL ON LEAF-LITTER SPIDER COMMUNITIES AT TWO ELEVATIONS

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ABSTRACT. This study investigates the indirect effects of primary productivity enhancement via fertilization, and the direct effects of environmental differences at two elevations, on the density and species richness of leaf-litter spiders. Litter was sampled in tabonuco forest (340–360 m elevation) and elfin forest (1051 m elevation) within the Luquillo Experimental Forest Long Term Ecological Research (LTER) site in Puerto Rico. Treatments consisted of three blocks with fertilization and control plots at both sites, and a one time removal of hurricane generated debris at tabonuco forest only. Treatments had no significant effect on spider density, species diversity, and species richness at either elevation. Elfin forest showed lower densities and lower species richness than tabonuco forest due to harsh environmental conditions. The thin litter layer and similar standing litter in the tabonuco forest suggest that spiders are limited by habitat, and also that they have successfully recolonized the debris cleared areas at this elevation. Harsh environmental conditions at elfin forest seem to be strong enough to counteract the effects of fertilizer addition on the measured variables. However, the high biomass of grasses in the fertilization plots at elfin forest could have caused an underestimation of spider densities. This study suggests that habitat availability is an important variable in bottom-up models for food web link control.

Keywords: Leaf-litter community, species diversity, primary productivity enhancement, tabonuco forest, Puerto Rico

Most studies of indirect effects of primary productivity enhancement on spider densities, or studies on spider recolonization patterns, have focused on above-ground spiders because they are easy to manipulate and count (Vince et al. 1981; Ehman & MacMahon 1996). Prey density may be affected by the bottom-up effects of nutrient addition in a food web (Power 1992). For example, the density of spiders of the Gulf of California is correlated negatively with island size (Polis & Hurd 1995). Higher marine productivity input to smaller islands, due to exposition of larger superficial area of small islands compared to larger ones, permits the support of higher arthropod prey densities and a higher density of web building spiders (Polis & Hurd 1995). In a salt marsh fertilization experiment, spiders showed a numerical response to an increased density of herbivores in the fertilization plots (Vince et al. 1981).

An increase in prey triggers a density independent aggregational and reproductive nu-

merical response in web-building spiders (Riechert & Lockley 1984; Wise 1993). These responses are said to be density independent because spiders have longer generation times and lower fecundity than most of their prey, and therefore can not track their prey populations closely (Riechert & Lockley 1984).

Spiders can quickly recolonize shrubs from which they are excluded by manipulation (Ehman & MacMahon 1996). Differences in the recolonization pattern, with an initial colonist inhibiting the establishment of others (see Drake 1991; Law & Morton 1993), have been shown to be an important factor in community composition development (Ehmann & MacMahon 1996).

As generalist predators, spiders constitute a very important group structuring leaf-litter communities (Clarke & Grant 1968; Moulder & Reichle 1972; Pfeiffer 1996). Leaf-litter arthropod communities can vary seasonally (Frith & Frith 1990), and along elevational gradients (Olson 1994). Variation in invertebrate abundance can also be related to availability of nutrients (Uetz 1976; Olson 1994) and fluctuations in environmental conditions

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(Frith & Frith 1990). The poorer the available nutrients and/or the harsher the environment, the lower the abundance.

In this study I focus on leaf-litter spiders to address the following questions: (1) How do harsh environmental conditions and lower primary productivity at one of two elevations of a tropical rain forest adversely affect litter spiders density and richness of species? (2) How does enhanced productivity at the two elevations, via fertilizer addition, favor higher densities of spiders?, and (3) How is species composition affected by recolonization of spider depleted sites?

I sampled litter spiders at two elevations in the Luquillo Experimental Forest (LEF). These two areas have subjected to fertilization treatments since 1989, after the strike of Hurricane Hugo. The low elevation site includes plots where all hurricane-generated debris was experimentally removed; and as a result, almost all invertebrates were also removed.

METHODS

Study site.—This study was conducted in the tabonuco and elfin forests found in the Luquillo Experimental Forest Long-term Ecological Research (LTER) site in Puerto Rico. The tabonuco forest area is located near El Verde Field Station, at the eastern part of Puerto Rico (18°20'N, 65°49'W) and it is at an elevation between 340–360 m (Zimmerman et al. 1995). It is classified as a subtropical wet forest (Ewel & Whitmore 1973). This area is dominated by *Dacryodes excelsa* Vahl, known as tabonuco, and *Prestoea montana* Nichols, known as the sierra palm (Walker et al. 1996).

The tabonuco forest was heavily damaged by Hurricane Hugo in September 1989 (Sanford et al. 1991). The mass of fine litter (defined as all leaf, wood <1 cm in diameter, and miscellaneous plant material) that resulted from the hurricane was almost 400 times the daily average at El Verde and Bisley (Lodge et al. 1991). Input of nutrients via litterfall appears to have altered nutrient cycles, increasing forest productivity and nutrient availability (Sanford et al. 1991). Canopy cover and height also decreased dramatically (Brokaw & Gear 1991). Invertebrate populations were greatly reduced (Alvarez & Willig 1993; Willig & Camilo 1991).

One of the elfin forest areas of the Luquillo Mountains is located at Pico del Este

(18°16'N, 65°45'W), which is a summit area at 1051 m of elevation. Its vegetation is classified as lower montane rain forest (Ewel & Whitmore 1973). The dominant species are *Tabebuia rigida* Urban, *Ocotea spathulata* Mez, and *Calyptanthus krugii* Kiaersk (Walker et al. 1996). This forest was heavily defoliated by Hurricane Hugo (Brokaw & Gear 1991). Compared to pre-hurricane levels, mean annual litterfall was 1.9 times higher, and the annual fine litterfall input of N (1.5×), P (1.7×) and K (3.1×) times higher (Lodge et al. 1991). Aside from these damages, there were no large structural changes at Pico del Este (Walker et al. 1996).

Structural and dynamic features of the tabonuco forest are very different from the high altitude elfin forest. The number of trees per hectare, basal area, and soil organic matter are higher in the elfin forest; while specific leaf area, canopy height, tree diameter range, forest volume and biomass, and species diversity are higher at the tabonuco forest (Weaver & Murphy 1990). Tree ingrowth and mortality, tree growth (includes biomass, volume, and diameter), litterfall, amount of loose litter, litter turnover, herbivory, and net primary productivity are higher at the tabonuco forest (Weaver & Murphy 1990). Climatic conditions in the elfin forest at Pico del Este such as high humidity, soil saturation, relatively low temperatures, high winds, and soil leaching are thought to be influential to its structural and dynamic features (Weaver et al. 1986, Weaver & Murphy 1990).

Experimental design.—The experimental blocks in the tabonuco forest were chosen at random. Each block was divided in three experimental plots measuring 20 × 20 m each (Zimmerman et al. 1995). Plots were located on ridge tops to minimize water flow between plots (G.R. Camilo pers. comm.). The three treatments were: (1) one-time total debris removal, (2) fertilization, and (3) control. The one-time debris removal treatment occurred one month after the hurricane. Following the treatment, litter was allowed to accumulate naturally. Fertilizer treatment was first applied immediately after Hugo and then approximately every three months. Fertilizer was added at an annual rate of 300 kg/ha N, 100 kg/ha P, 100 kg/ha K, 8 kg/ha B, 15.4 kg/ha Cu, 2.2 kg/ha Fe, 25 kg/ha Mn, 26 kg/ha Zn and 19 kg/ha Mg (Walker et al. 1996). These rates

constitute N (3×), P (30×) and K (2×) the mean annual inputs from fine litterfall (Lodge et al. 1991). The control plot was left intact, with no debris removed and no fertilizer applied (Walker et al. 1996).

Each block in elfin forest consisted of pairs of plots, located on ridge tops, randomly assigned as control or fertilization (Walker et al. 1996). Debris removal treatment was not applied due to the small amount of Hurricane generated debris at this forest (Zimmerman pers. comm.). Each plot measures 9 × 14 m. Fertilizer was first applied in April 1990 and then every 3 months to the present (Walker et al. 1996). Fertilizer constitute N (15×), P (166×), and K (30×) the mean annual input from leaf litterfall (Lodge et al. 1991). For this study I used three adjacent blocks in elfin forest to compare with three blocks in the tabonuco forest.

The litter spider community was sampled five times at each site between February 1996–January 1997. Each sample consisted of four random 0.25 m² quadrants of leaf litter taken by hand from each experimental plot in each of three blocks at tabonuco forest and six randomly chosen plots at elfin forest. Leaf litter was then taken to the laboratory and placed in Berlese funnels for 5 days, or until dry, to extract invertebrates. After invertebrates were removed the processed litter was returned to the site of collection.

We placed four pitfall traps randomly in each plot in order to sample wandering nocturnal spiders and other invertebrates that may not retreat into the leaf litter by daytime. Traps consisted of containers with openings of 10 cm in diameter and 18 cm deep. Each container was filled to less than half of its capacity with a 70% ethanol -5% ethylene glycol solution. The opening was covered with disposable dish to exclude rain water. The traps were left on the sites for two days.

Spider samples obtained from Berlese and pitfall traps were preserved in 70% ethanol and were sorted by family and genus, and identified to species whenever possible using the appropriate literature (Petrunkevitch 1929, 1930a, 1930b; Bryant 1942; Chickering 1967, 1968, 1969, 1972a, 1972b). Juveniles were identified to family level only. Family and generic names follow Platnick (1989). Collected specimens were deposited in the Biology Mu-

seum of the University of Puerto Rico, Río Piedras Campus.

ANOVAs for a two-factor split plot design laid off in localities (based on Ott 1993) were performed to determine differences in square root transformed density data (Zar 1984) and the number of species present between treatments and localities. Subplots within a locality were tested for treatment and time of sampling effects. In addition, two-factor repeated measures ANOVA (Ott 1993) were performed on data from tabonuco forest to include data from the debris removal treatment, which is excluded in the split plot ANOVA.

The Morisita-Horn index was used to estimate the similarity (family level) among sites (Horn 1966; Wolda 1983; Russel-Smith & Stork 1995). A Multidimensional Scaling analysis was performed on the similarity matrix obtained from the index calculations to have a graphic representation of the dissimilarities between plots. A Principal Components Analysis was performed on data from all sites to determine which families are more important to the dissimilarities between plots.

RESULTS

Density of spiders.—A split plot ANOVA performed on data from both sites showed that there is no effect of treatment on spider density, but there is significant difference between localities (Table 1a). Densities per plot ranged from 0–15 ind./m² at elfin forest and from 5–118 ind./m² at tabonuco forest (Fig. 1). A repeated measures ANOVA performed on data from tabonuco forest to account for debris removal treatment effects revealed no difference in density of spiders between treatments, but revealed effects of time (Table 1b). Peak densities occurred between September and October (Fig. 1).

Species richness.—Based on adult individuals, there was a total of 31 species and 19 families identified from the two forest types (Table 2). A total of 27 species was found at tabonuco forest (Table 2). The dominant species in all treatments was *Modisimus montanus*, followed by *Theotima radiata*, and *Mastetia petrunkevitchi*. When juveniles and adults were taken together, the dominant family was Pholcidae (Table 2). *Modisimus montanus* is the only adult species collected in the Pholcidae, therefore the juvenile individuals are probably of the same species.

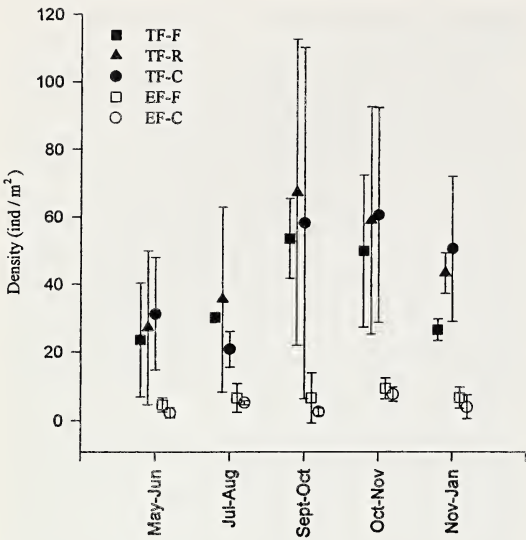


Figure 1.—Density of spiders per treatment plot, elevation, and sampling date. TF = tabonuco, EF = elfin, F = fertilization, R = debris removal, C = control.

Data from elfin forest yielded 16 species, four of these were found only at elfin forest; and all four of these were collected only once (Table 2). Pooled data for adult individuals

from both treatments show that *Mysmena caribbaea* is the dominant species at this locality, followed closely by *Oningis minutus* and *Corinna jayuyae* (Table 2). *Theotina radiata* and *M. petrunkevitchi* were virtually absent at elfin forest. When juveniles are taken in consideration, along with adults, the dominant families are Pholcidae (presumably *M. montanus*) and Salticidae (most adults represented by *O. minutus*) (Table 2). Of the seven species collected only in pitfall traps at tabonuco forest, *Agriognatha gloriae* was a web builder not typical of the litter, but of the understory. At elfin forest there were two species captured only in pitfall traps (Table 2). Of the two species, a poorly-preserved male specimen of the genus *Tetragnatha* is typical of the understory.

A split plot ANOVA showed that the number of species differed between localities but not between treatments (Table 3a). The number of species was higher at tabonuco forest (see Table 2). A repeated measures ANOVA, performed on data from tabonuco forest to account for debris removal effects, revealed no effect of this treatment on the number of species (Table 3b).

Community similarity.—The Morisita-

Table 1.—ANOVA analysis for the effects of treatment, time of sampling, and elevation on the density of leaf litter spiders. TF = tabonuco, EF = elfin.

Source	df	Mean square	F	P
A. Split plot ANOVA to compare treatment and time of sampling effects between TF and EF. Debris removal was excluded from this analysis.				
Between localities				
Time	4	5.402	1.72	>0.25
TF vs EF	1	228.32	72.64	<0.0025
Time × (TF vs EF)	4	3.143		
Within localities				
Treatment	1	0.025	0.01	0.904
Treatment × Time	4	0.546	0.32	0.865
Error	45	1.723		
B. Repeated measures ANOVA to compare effects of treatment (including debris removal) and time of sampling (Time) at the plots of tabonuco forest.				
Between blocks				
Treatment	2	1.334	1.46	>0.25
Plots in treatment	6	0.910		
Within blocks				
Time	4	11.66	3.01	0.035
Time × Treatment	8	0.935	0.24	0.979
Error	24	3.88		

Horn community similarity index was calculated using pooled data for family from all sampling times. Table 4 shows the similarity matrix obtained from this analysis. Multidimensional Scaling Analysis of the matrix shows good separation of sites based on locality (Fig. 2). Plots from the same elevation and treatment tend to be most closely related, with the exception of the tabonuco forest, where removal plots show the greatest variation in species composition (Fig. 2). Principal Component Analysis show that the first axis accounts for 92% of the variance between plots. The family with the highest absolute loading in this axis is Pholcidae (0.98), followed by Ochyroceratidae (0.15) and Heteropodidae (−0.085). Axis 2 accounts for 4.2% of the variance between plots, with the highest absolute loading values for Ctenidae (−0.73), Heteropodidae (−0.66) and Pholcidae (−0.35). Axis 1 shows a clear separation of plots by elevation, except for two plots from tabonuco forest (control #2 and debris removal #3) that appear together with the plots from elfin forest (Fig. 3). These two plots from tabonuco forest have a lower density of Pholcidae than the rest of the plots from this elevation. Axis 2 clearly separates one of the fertilized plots from elfin forest from all the other plots (Fig. 3). The prevalence of families with negative eigenvector values (namely Oonopidae, Ctenidae and Heteropodidae) is responsible for this separation.

DISCUSSION

Density of spiders.—The lack of a treatment response may be due to a lack of response from spider prey to treatments. Preliminary data for litter insects from the same experimental plots show no significant difference between treatments at tabonuco forest or elfin forest (E. Nazario pers. comm). Standing litter was similar for all treatments at a given elevation, even though litter fall was higher in fertilization plots at each elevation site (Walker et al. 1996). This suggest that there is a higher density of decomposers in the fertilization plots.

A factor opposing the bottom-up productivity enhancement effects on spiders relates to features of the litter. The structure and depth of the litter have been shown to be very important factors affecting the density and diversity of litter arthropods (Uetz 1979; Bult-

man & Uetz 1982, 1984). Spider density and diversity increase with higher litter depth and complexity (Uetz 1979; Bultman & Uetz 1982, 1984). Litter depth proved to be more important, in the short term, for spiders than nutrient content of the litter (Bultman & Uetz 1984). The fact that the litter layer is relatively thin at the tabonuco forest (Pfeiffer 1996) and elfin forest (pers. obs.), and that standing litter in our plots is similar in all treatments (Zimmerman et al. 1995; Walker et al. 1996), supports the statement that spiders are habitat limited in our plots. The constant and rapid turnover of leaf litter (La Caro & Rud 1985) may limit habitat for litter spiders. Because leaves are constantly decomposing, *M. montanus* will have to frequently switch to a new leaf.

Consumption by vertebrate predators is not a very important factor opposing the bottom-up productivity enhancement effects on litter spiders in the tabonuco forest (Pfeiffer 1996). Diurnal predators concentrate foraging activities to the arboreal layers (Reagan 1996); nocturnal predators forage in arboreal areas or near the ground (Stewart & Woolbright 1996). *Eleutherodactylus portoricensis* Schmidt is the only vertebrate that includes some litter arthropods in its diet (Stewart & Woolbright 1996). Non-anoline reptiles like the gecko *Sphaerodactylus klauberi* Grant (1 individual/m²) may account for the majority of litter arthropod consumption (Pfeiffer 1996), which include, in order of quantity, Acari, Araneae, Collembola, Isopoda, and Coleoptera (Thomas & Gaa Kessler 1996). However, unlike *Eleutherodactylus* frogs, we never collected *S. klauberi* in the litter.

The one time debris removal from experimental plots in 1989 eliminated almost all litter fauna and their respective habitats. The lack of differences in spider density, and the similarity of standing litter between treatments (Zimmerman et al. 1995), suggests that litter spiders were able to recolonize rapidly. Spiders near the debris removal plots had potential free habitat to colonize from the moment when leaf fall began to cover the forest floor once again. The similarity of standing litter between treatments (Zimmerman et al. 1995) meant equal leaf-litter habitat availability in all plots. The relatively small size of our study plots (20 m²) permits rapid recruitment of col-

Table 2.—Pooled abundance for spider families and species found in all treatments at the sites of tabonuco (TF) and elfin (EF) forests. Data include total number adult and juvenile specimens collected in Berlese funnels for each family. Total number of individuals from a species is based on adult individuals only. Species found only in pitfall traps are indicated by an asterisk (F = fertilization, R = debris removal, C = control).

Taxon	TF-F	TF-R	TF-C	EF-F	EF-C
Pholcidae	351	426	358	36	4
<i>Modisimus montanus</i> Pet.	67	87	79	8	1
Ochyroceratidae	32	91	48	4	4
<i>Ochyrocera</i> sp.	0	0	1	1	2
<i>Theotima radiata</i> Simon	23	72	37	0	0
Dipluridae	44	25	47	0	0
<i>Masteria petrunkevitchi</i> (Chickering)	18	8	11	0	0
Corinnidae	46	46	45	11	7
<i>Corinna jayuyae</i> Pet.	6	8	9	3	2
<i>Trachelas bicolor</i> Keyserling*	1	0	0	0	0
Heteropodidae	44	13	35	6	4
<i>Pseudosparianthis jayuyae</i> Pet.	7	0	4	1	2
Salticidae	20	23	36	12	28
<i>Corythalia glorieae</i> Pet.	5	4	8	0	0
<i>Emanthis portoricensis</i> Pet.	0	0	0	0	1
<i>Oningis minutus</i> Pet.	0	1	3	5	7
Oonopidae	17	3	22	7	2
Close to <i>Dysderina</i> sp.	1	0	0	0	1
<i>Oonops ebenicus</i> Chickering	4	1	7	1	0
<i>Oonops</i> sp.	1	0	1	0	0
Close to <i>Opopaea lutzi</i> Pet.	3	0	3	4	0
<i>Stenoonops</i> sp.*	2	0	0	0	0
Ctenidae	11	6	4	8	7
<i>Celaetycheus strennus</i> Bryant	0	1	0	4	1
<i>Oligoctenus otleyi</i> Pet.	1	1	0	0	0
Symphytognathidae	0	5	2	9	5
<i>Mysmena caribbaea</i> Gertsch	0	2	2	9	4
Barychelidae	16	7	5	1	0
<i>Trichopelma corozali</i> (Pet.)	8	7	5	1	0
Caponidae	0	0	3	4	1
<i>Nops blanda</i> (Bryant)*	0	0	1	2	0
Hahniidae	0	2	7	0	0
<i>Neohahnia ernesti</i> (Simon)	0	2	0	0	0
Linyphiidae	0	7	0	0	0
<i>Leptyphantes microserratus</i> Pet.	0	6	0	0	0
Liocranidae	4	0	2	0	0
<i>Phrurolithus insularus</i> Pet.	3	0	2	0	0
Prodidomidae	1	0	1	0	0
<i>Lygromma</i> sp.*	1	0	0	0	0
Tetragnathidae	1	0	0	1	0
<i>Agriognatha glorieae</i> Pet.*	1	0	0	0	0
<i>Tetragnatha</i> sp.*	0	0	0	1	0
Theraphosidae	1	1	0	0	0
<i>Ischnocolus culebrae</i> Pet.*	0	1	0	0	0

Table 2.—Continued.

Taxon	TF-F	TF-R	TF-C	EF-F	EF-C
Theridiosomatidae	1	5	7	1	4
<i>Baalzebub albinotatus</i> (Pet.)	0	0	0	1	0
<i>Chthonas</i> sp.	0	2	3	0	0
<i>Styposis luteus</i> (Pet.)	0	0	0	0	1
Thomisidae	0	1	1	0	0
<i>Epicaudus mutchleri</i> Pet.	0	1	1	0	0

onizers from the surrounding habitat limited leaf litter.

Difference in density of litter spiders between tabonuco forest and elfin forest is consistent with a study that compared abundance and diversity of litter arthropods at different elevations in Panama (Olson 1994). In western Panamanian forests, species diversity and number of individuals decline in the upward transition to cloud forests (Olson 1994). This decline is associated with harsher environmental conditions (Weaver et al. 1986; Olson 1994), lower productivity (Weaver & Murphy 1990), and low resource availability (Olson 1994) at high elevations. Some harsh climatic conditions at elfin forest include high humid-

ity, moisture saturation, relatively low temperatures, high winds, and soil leaching (Weaver et al. 1986). Primary productivity (Weaver & Murphy 1990) and insect density (E. Nazario pers. comm.) are also lower at PE compared to EV. Leaf litterfall (Weaver & Murphy 1990) and standing litter (Walker et al. 1996) is also lower for PE. Thicker leaves at PE (Medina et al. 1981) should also be harder to curl than leaves at EV; and this could reduce the three-dimensional space of the litter, which is an important feature for spider habitat (Uetz 1979; Bultman & Uetz 1984).

Species richness.—Another study done at tabonuco forest found a total of 22 spider spe-

Table 3.—ANOVA analysis to compare the effects of treatment and time of sampling between tabonuco (TF) and elfin (EF) forest on the number of species.

Source	df	Mean square	F	P
A. Split plot ANOVA to compare treatment and time effects between elevations. Debris removal is excluded from the analysis.				
Between elevations				
Time	4	3.52	2.32	>0.10
TF vs EF	1	104.017	68.58	<0.0025
Time × (TF vs EF)	4	1.52		
Within elevations				
Treatment	1	3.75	0.17	0.68
Treatment × Time	4	3.08	1.94	0.12
Error	45	1.59		
B. Repeated measures ANOVA to compare treatment (debris removal included) and time of sampling at the plots of tabonuco forest.				
Between blocks				
Treatment	2	1.09	0.23	>0.25
Block	6	2.48		
Within blocks				
Time	4	2.86	1.47	0.24
Time × Treatment	8	2.01	1.03	0.43
Error	24	1.94		

Table 4.—Morisita-Horn community similarity index calculated for pooled data from each treatment plot. Numbers after treatment codes represent block number. Number of families per plot is given in the diagonal, shared species between plots are given in the upper right corner. Legend as in Table 1.

	EF	EF	EF	EF	EF	TF	TF	TF	TF	TF	TF	TF	TF	TF	TF	TF	TF	TF	TF	TF	TF
	F1	F2	F3	C1	C2	C3	F1	F2	F3	R1	R2	R3	C1	C2	C3	R1	R2	R3	C1	C2	C3
EF-F1	10	6	6	8	5	7	8	8	6	9	9	8	7	8	9						
EF-F2	0.76	7	6	7	5	5	5	5	5	6	6	6	5	6	7						
EF-F3	0.60	0.50	8	8	4	6	6	5	6	7	6	7	6	7	8						
EF-C1	0.86	0.70	0.76	10	5	8	7	7	7	9	8	9	8	9	10						
EF-C2	0.82	0.81	0.52	0.81	5	4	5	5	5	5	5	5	4	5	5						
EF-C3	0.64	0.47	0.60	0.81	0.72	8	6	6	6	8	7	8	7	7	8						
TF-F1	0.79	0.79	0.60	0.62	0.74	0.45	13	8	10	9	8	9	8	9	11						
TF-F2	0.65	0.77	0.36	0.45	0.58	0.28	0.86	10	8	9	9	8	7	9	9						
TF-F3	0.73	0.87	0.48	0.59	0.77	0.44	0.92	0.92	10	9	8	8	8	9	10						
TF-R1	0.74	0.82	0.39	0.57	0.67	0.35	0.85	0.91	0.93	12	10	11	9	10	12						
TF-R2	0.69	0.82	0.32	0.47	0.60	0.26	0.82	0.94	0.93	0.97	11	10	8	9	10						
TF-R3	0.81	0.84	0.52	0.79	0.87	0.66	0.77	0.70	0.8	0.74	0.69	14	9	9	12						
TF-C1	0.71	0.88	0.40	0.59	0.69	0.41	0.86	0.89	0.96	0.94	0.94	0.76	10	8	10						
TF-C2	0.77	0.72	0.62	0.74	0.84	0.69	0.85	0.76	0.82	0.75	0.67	0.84	0.72	11	11						
TF-C3	0.74	0.82	0.55	0.63	0.67	0.38	0.91	0.93	0.95	0.94	0.92	0.78	0.92	0.82	16						

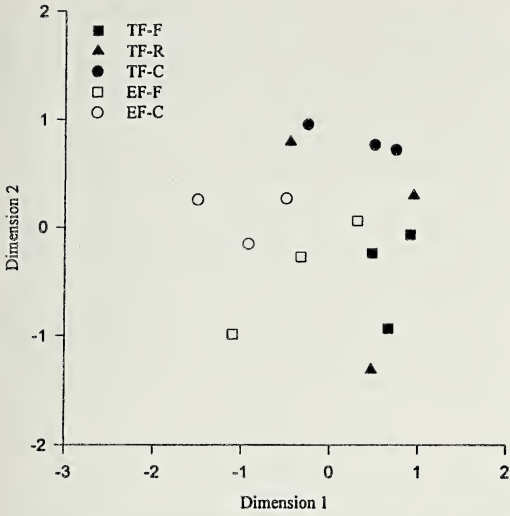


Figure 2.—Multi-dimensional Scaling Analysis on the Morisita-Horn community similarity index (stress = 0.222). TF = tabonuco, EF = elfin, F = fertilization, R = debris removal, C = control.

cies in the leaf litter (Pfeiffer 1996). The higher number of species I found was the result of using pit-fall traps. The dominant species in tabonuco forest are consistent with the dominant species found by Pfeiffer (1996). The difference in dominant species I found between elevations has been found in other studies (Olson 1994), and is related to the same conditions that limit density (see previous section).

Community similarity.—Differences in community composition between elevations are related to differences in environmental conditions (Olson 1994). Dissimilarity between debris removal plots is indicative of random differences in the recolonization pattern at each of the plots, with an initial colonist species inhibiting the establishment of others (see Drake 1991; Law & Morton 1993). Differences in the initial colonists arriving to a spider depleted plot have been shown, in the short term, to be important in the process of community development (Ehmann & MacMahon 1996). Principal Components Analysis showed that differences between plots was mainly explained by differences in the abundance of Pholcidae. Lower Pholcidae abundance in a tabonuco forest removal plot and a control plot (Fig. 3) grouped them with plots from elfin forest. The difference of Pholcidae abundance in these two plots is likely to be due to the heterogeneity between plots.

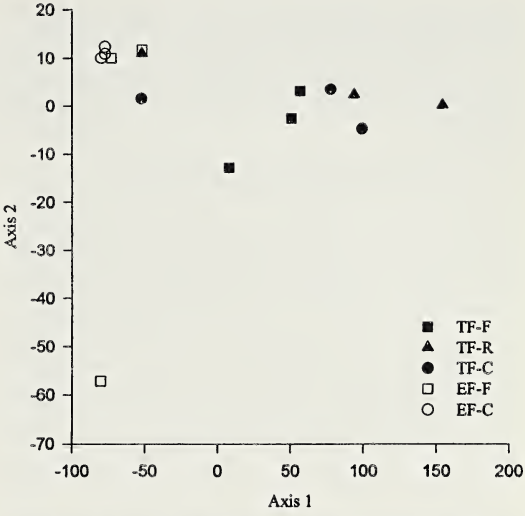


Figure 3.—The distribution of treatment plots in a two-dimensional morphospace, based on scores from the first two family principal components axes. TF = tabonuco, EF = elfin, F = fertilization, R = debris removal, C = control.

Higher numbers of individuals of some families at elfin forest compared to tabonuco forest (Table 2) are indicative of differences in community structure between both elevations. Dissimilarity between elevations is consistent with the steady changes in community composition, or species turnover, found in an elevational gradient in Panamanian forests (Olson 1994). Analysis of species composition at the intermediate forests of El Yunque (palm and colorado forests) is necessary in order to determine if species turnover is constant.

Morisita-Horn analysis was also applied to determine similarity between mean annual density (MAD) data from Pfeiffer (1996) and my pooled treatments mean density per sample (PMD) data for tabonuco forest. The calculated index was 0.92. In order to determine how his data compare to mine in terms of density of individuals from each family, I ran a simple regression analysis. This analysis showed a high correlation of his data with mine ($r = 0.90$, $P < 0.0005$). However, Pfeiffer (1996) found a higher density of spiders than I did ($MAD = 5.94 + 1.90 * PMD$). The higher density of spiders found by Pfeiffer (1996) can be attributed to selection of sample sites away from rock surfaces and his use of a vacuum aspirator to obtain his samples. Our treatment plots were located along ridge tops.

This feature can minimize the already thin litter cover on the steeper areas, while concentrating litter on the relatively flat areas, consequently minimizing litter obtained for analysis.

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A TWENTY-YEAR COMPARISON OF EPIGEIC SPIDER COMMUNITIES (ARANEAE) OF DANISH COASTAL HEATH HABITATS

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ABSTRACT. The same epigeic spider communities of North-west Jutland coastal heath habitats (Denmark, region Thy) initially surveyed by pitfall traps from 1977–79 were examined 20 years later (1997–98). The heath plots were open sandy areas growing into *Calluna* heath, and the more stable *Erica*, *Calluna/Empetrum*, *Molinia* vegetation types. They have changed vegetatively only a little in those 20 years from natural succession. Though the spider communities of all areas showed only minor changes from the passage of time, these were larger than the differences attributable to the different habitat types despite large differences in soil humidity and vegetation structure.

Keywords: Spiders, community composition changes, coastal heathland habitats, Denmark

The impact of habitat management on spider communities is usually analyzed by comparing variously treated or disturbed/undisturbed sites at the same point in time. Other studies have followed changes in the spider fauna associated with specific disturbances and the subsequent successional recovery by collecting over a series of years (heathland fires: Merrett 1976; forest fires: Huhta 1971, Schaefer 1980). Studies of long-term changes in the spider fauna of a particular site due to human modification of the biotope, pollution, vegetational succession, climatic change, or other causes are rare. Schikora (1994) found relatively minor changes over 22 years in the spider species of a bog in spite of prominent vegetation changes due to drainage. However, the dominant spiders had changed from photophilous to skotophilous species. Hänggi & Maurer (1982) compared the spider fauna of a Swiss raised bog after a 50-year interval, but the collecting methods were different. No known studies has analyzed the spider fauna of a specific locality by comparable methods over a long temporal scale.

Our aim in the present study is to compare the epigeic spider communities of four adjacent Danish coastal heathland habitats sampled by pitfall traps in the same locations with an interval of 20 years. We compare similarities in community composition both between

habitats and between time periods. The vegetation of the area was only slightly affected by human activity in the intervening time. One site, which had been disturbed at the time of the first investigation, had been changed by vegetational succession during the 20 years.

METHODS

Site descriptions.—The study was carried out at Tørvekjær by Vester Vanned Sø, Thy, Denmark (57°1'30"N, 8°32'E). The area consisted of coastal heathland patches between an oligotrophic marsh to the south and sandy pastures and a coniferous plantation to the east and west. The plantation was established in the late 1950's and has provided increasingly more protection from the wind as it matured. The North Sea coast is ca. 3.5 km to the west.

Four points were sampled on a N-S transect perpendicular to low sandy ridges deposited by the prevailing westerly winds, which created alternating depressions and "hills" with varying vegetation. The differences in height between hills and depressions were never more than 0.5 m. However, the depressions could flood during winter, resulting in very divergent vegetational characteristics at the sites.

Traps 1–2 were situated on a hilltop, 3 m from the edge of a spruce plantation. In 1977–79 the traps were placed in a patch of bare

sand created by human disturbance. In 1997 the vegetation had recovered completely and grown into a typical dry heathland patch, dominated by *Calluna vulgaris* (L.) (coverage 50%), *Empetrum nigrum* L. (30%), and moss as groundcover.

Traps 3–4 were in a moist depression, 17 m from traps 1–2. The vegetation was dominated by *Erica tetralix* L. (90%) with moss covering the ground, and showed no recognizable changes between the two sampling periods.

Traps 5–6 were on a hilltop, 9 m from traps 3–4. The general character of the vegetation was dry dwarf-shrub heath. In 1977–79 it consisted of a mixture of *Calluna* and *Empetrum*; in 1997 *Empetrum* (70%) with moss groundcover was clearly dominant.

Traps 7–8 were in the next depression, 17 m from traps 5–6. In both sampling periods the vegetation was a nearly-pure dense stand of the low grass *Molinia caerulea* (L.) (>90%), indicating a very moist soil. Whereas the first three sites were dwarf-shrub heaths, this site was better characterized as a meadow.

Trapping.—Pitfall traps were used to monitor the active densities of ground-dwelling spiders at the selected sites. In 1977–79 glass jars (diameter 8 cm) were used, but in 1997 we used plastic beakers fitted into plastic flower pots (diameter 11 cm). A 3% formalin solution with ethylene glycol and detergent was used as a killing agent and preservative on both occasions. Trapping periods were 7 May 1977–23 March 1978, 13 May 1978–17 March 1979, and 11 May 1997–21 March 1998. The traps were emptied every 2–3 weeks during the warm seasons, and once a month or more infrequently during the winter periods.

Pitfall traps were placed in pairs at each site ca. 1–2 m apart. When trapping was repeated in 1997–98 the new traps were placed as close as possible to the same positions as was used earlier, all probably less than 2 m away.

The spider material is deposited in the collection of Zoological Museum, Copenhagen.

Weather.—We obtained weather information from the Danish Meteorological Institute. For 1977–79 data are from station Silstrup, for 1997–98 from Hørsted. Both are ca. 15 km from the study area. We used the monthly averages of temperature, sunny hours, and rainfall (Fig. 1).

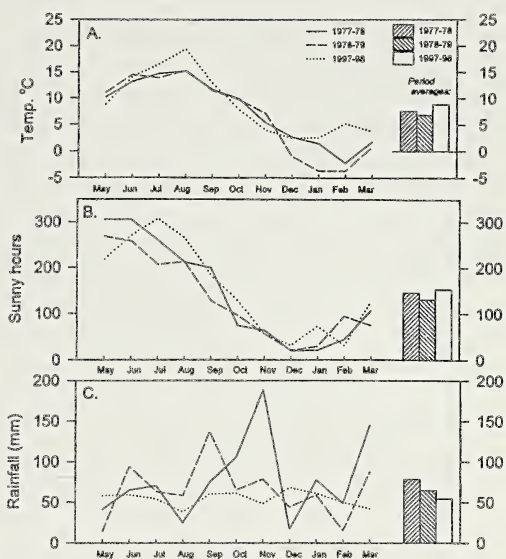


Figure 1.—Weather conditions during the three study periods, all plotted as monthly averages. A: Temperature (°C), B: Hours of sunshine, C: Rainfall (mm).

Overall 1997–98 was somewhat sunnier and warmer and with less precipitation than 1977–79. The average differences between the three trapping periods are quite small, and the conditions of 1997–98 do not deviate more from either of the early periods than from each other (Fig. 1).

Data analysis.—Comparison of the epigeic spider communities was made by Principal Component Analysis (PCA) using the CANOCO program (ter Braak 1987; cf. Jongman et al. 1987). We compared the summed catches for each site and catching period and applied the PCA to log-transformed abundances of each species. All species were included in the analyses (and thus in determining the relative distribution of the trap sites (Fig. 2)), but only the most dominant species (> 2% at one site and period) are presented in the species plot (Fig. 3). We also illustrate the species that disappeared or appeared between 1977–79 and 1997–98, as well as less dominant species (though > 0.4%) which showed substantial changes in relative abundance (Fig. 4). Additionally, we compared the dominance structure and species composition of the habitats (Fig. 5), and analyzed the species changes between the two periods. Two similarity indices for pairwise comparisons (Southwood 1966) were calculated: the Sørensen Quotient of

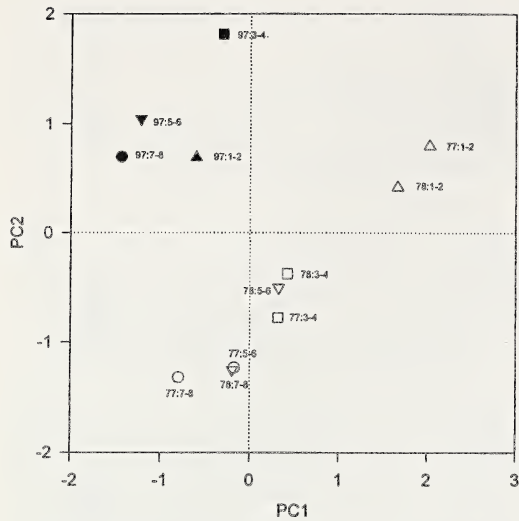


Figure 2.—Principal Component Analysis (site plot) of summed catches from each of four trap sites for three trapping periods (1977–78, 1978–79 and 1997–98). Starting year and trap-numbers indicated next to each point. Traps 1–2: Bare sand (1977, 1978) or *Calluna* (1997); Traps 3–4: *Erica*; Traps 5–6: *Empetrum/Calluna*; Traps 7–8: *Molinia*.

similarity, $QS = 2j/(a + b)$, where a and b are the number of species in the two samples, and j is the number of species common to both samples; and the Percentage of similarity, $\%S = \sum_i \min(p_{ia}, p_{ib})$, which sums the lowest values for the proportional abundances (p) of each species (i) in the two samples (a, b).

RESULTS

Faunistic characteristics.—A total of 6368 specimens belonging to 113 species was collected, of which 23 species had a relative dominance of >2% in at least one site and year. The number of individuals and species at each site increased for 1997–98 compared to the earlier periods (Table 1). It can therefore

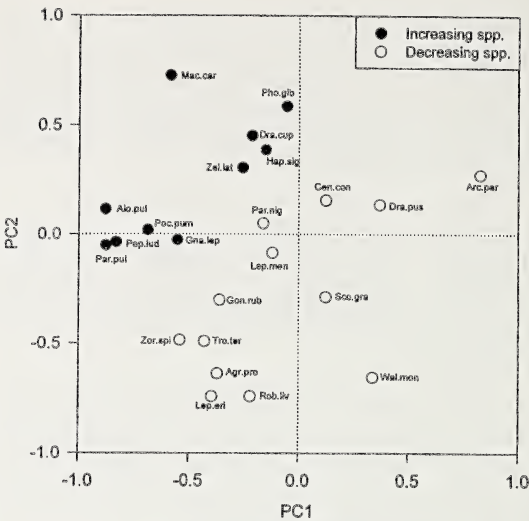


Figure 3.—Principal Component Analysis (species plot, same analysis as Figure 2) of summed catches from each of four trap sites for three trapping periods (1977–78, 1978–79 and 1997–98), illustrating dominant species (>2%). Abbreviations of species names: see Appendix 1.

be concluded that there has been no decline in the richness of the spider fauna over the 20 years.

The number of species in common between the trapping periods was extremely stable (Table 2). It is remarkable that the number of species disappearing between 1977–78 and 1978–79 was the same as between 1977–78 and 1997–98. This may indicate that “disappearance” does not necessarily mean extinction but rather reflects chance of capture. Given the low number of traps in each habitat, this effect is not surprising. More new species seem to have accumulated over the 20 year period than between 1977–78 and 1978–79, but this may also be due to the higher number of individuals caught in 1997–98.

Table 1.—The number of individuals and species of spiders collected by two traps at each of four trapping stations during the three trapping periods.

	1977–78		1978–79		1997–98	
	Ind.	Species	Ind.	Species	Ind.	Species
Traps 1–2	317	46	429	46	465	56
Traps 3–4	513	47	536	41	671	47
Traps 5–6	583	54	487	38	532	50
Traps 7–8	584	43	544	41	707	54
Total	1997	80	1996	71	2375	87

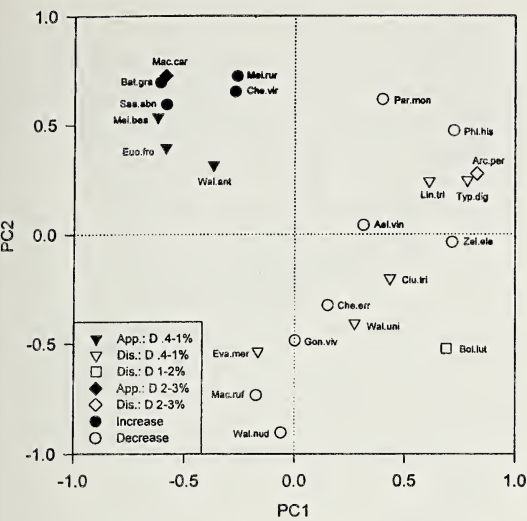


Figure 4.—Principal Component Analysis (species plot, same analysis as Fig. 2) of summed catches from each of four trap sites for three trapping periods (1977–78, 1978–79 and 1997–98), illustrating species appearing (App.) or disappearing (Dis.) between 1977–79 and 1997–98 (maximal dominance value (D) in year of presence indicated), and non-dominants showing substantial changes (increase/decrease) between these periods. Abbreviations of species names: see Appendix 1.

Principal component analysis.—Analysis of spider species abundances in each of the traps during every trapping period resulted in a plot of sites \times years (Fig. 2) and corresponding plots of species distributions (Fig. 3, 4). The sites clustered in three groups (Fig. 2). One group consisted of traps 1–2 from 1977–78 and 1978–79; a second group was formed by all other sites for the same two periods, and the third group included the four sites from 1997–98. Thus, except for traps 1–2 in the early periods, the habitats do not cluster together while the catching periods do. This means that the temporal changes in the fauna

are more prominent than the differences between the habitats. Axis 1 (PC1) mainly reflects the changes resulting from vegetational succession at traps 1–2, while axis 2 (PC2) reflects the faunistic changes taking place at the remaining trapping sites over 20 years, which cannot be easily related to specific habitat changes. There seem to be no further relationships between the two PC-axes and characteristics of the habitats. The change of the spider community at traps 1–2 was expected because this site was a disturbed patch of bare sand, which succession eventually turned into a plant community similar to that of site 5–6. We repeated this analysis for spring/summer (May–September) and autumn/winter (October–March) catches separately. Both data sets gave the same pattern as for the full periods.

The dominant species were concentrated in the central part of the PC-plot (Fig. 3), reflecting a high similarity in species composition between the habitats within a period. This plot and the following (Fig. 4) show the differences in species composition responsible for the pattern in Fig. 2, and the axes should be interpreted similarly. Species in the upper left are those that increased in abundance after 20 years, while those to the right and in the lower part decreased. Species that either appeared or disappeared during the 20 years or had a relative abundance of $< 2\%$ showed a clear separation of increasing/appearing vs. decreasing/disappearing (Fig. 4).

Both types of similarity indices between years produced values between 70–80% (Table 2). The two early periods were not more similar than early versus late periods.

Dominance structure.—The same few species were the dominants in all four habitats (Fig. 5), with *Gnaphosa leporina* (20) and *Centromerita concinna* (3) being at positions 1–3

Table 2.—Comparison of spider population characteristics between trapping periods (catches from different habitats summed for each year).

	77–78 vs. 78–79	77–78 vs. 97–98	78–79 vs. 97–98
Number species both periods	57	58	59
Number species disappearing	23	22	12
Number species appearing	14	27	28
Sørensen's quotient of similarity	75.5	70.3	79.7
Percent similarity	69.0	79.3	69.5

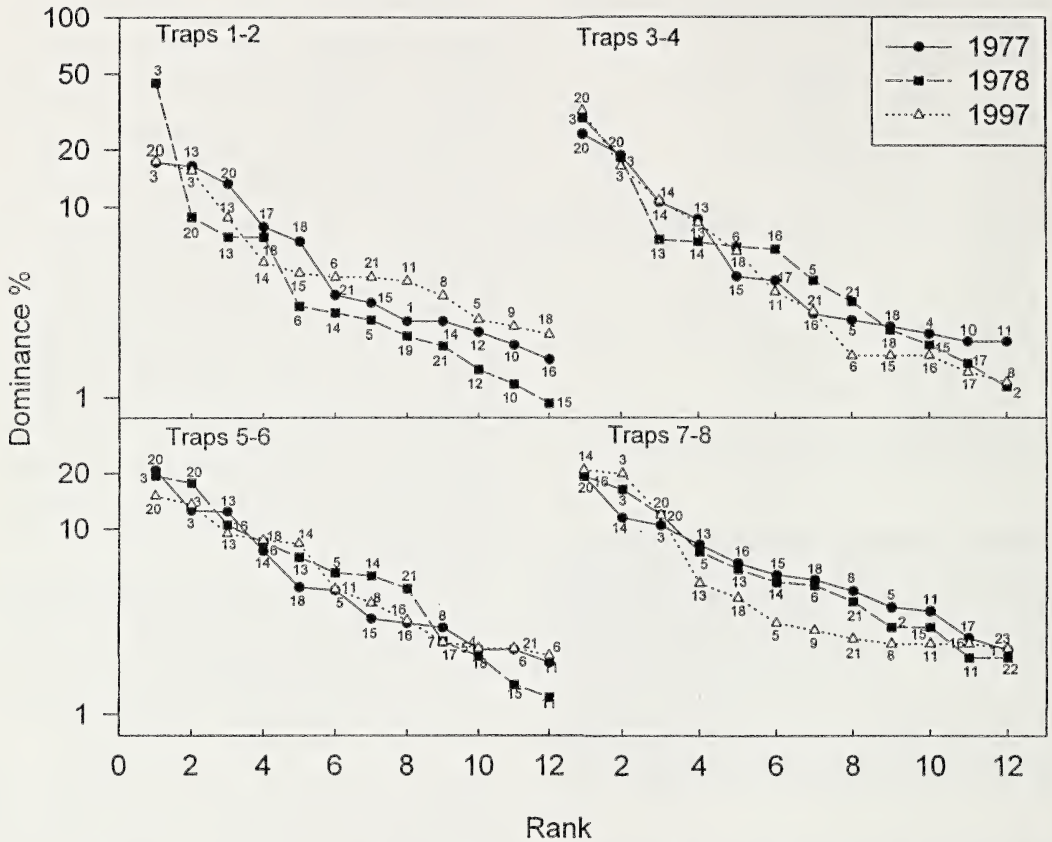


Figure 5.—Dominance curves for spider communities of four heathland trap-sites in three trapping periods (12 most abundant species only). Numbers indicate species identity (cf. Appendix 1).

in all habitats and years (Fig. 5). Only in the *Molinia* habitat they were surpassed by *Pardosa pullata* (14) and *Agroeca proxima* (16). *Pardosa nigriceps* (13) was codominant at the two "hilly" sites, while *P. pullata* had its highest dominance in the moist depressions. When comparing the four sites over the 20 years there are no indications of systematic changes in the dominance structure. Five species occurred with > 2% dominance in all years at all sites: *C. concinna*, *P. nigriceps*, *P. pullata*, *G. leporina*, and *Haplodrassus cupreus*.

Species appearances and disappearances.—At trap sites 1–2, several species preferring bare sandy areas were caught during 1977–79 but disappeared later when the vegetation closed. That was true for *Arctosa perita*, while *Pardosa monticola*, *Aelurillus insignitus* and *Zelotes electus* decreased in abundance. Some vegetation-dwelling species,

like *Linyphia triangularis* and *Philodromus histrio*, seemingly decreased. It is possible, however, that this is an artifact because they are found only on the soil surface if there is no vegetation.

Macrargus rufus declined at some sites while *M. carpenteri* appeared in considerable numbers in 1997–98. We are unable to relate this shift to the small habitat or environmental changes between the sampling periods. Increasing species (cf. Figs. 3, 4) include species that in Denmark are associated mainly with (dry) heathlands (*P. ludicrum*, *Z. latreillei*, *D. cupreus*), while others are hygrophilous (*M. beata*) or even moist heathland specialists (*G. leporina*).

Thus, it is impossible to determine a direction of change with respect to the ecological characteristics associated with species whose abundances changed.

DISCUSSION

Structural characteristics of the vegetation are generally thought to be the most important factor for habitat selection of spiders and thus for determining the composition of the spider fauna (Duffey 1962, 1966, 1968; Curtis & Bignal 1980; Robinson 1981). We therefore expected spider communities in different habitats to show large differences relative to the temporal changes, especially at the two sites where no vegetational changes had occurred. We observed the opposite in spite of great differences in vegetational physiognomy between some of the sites. The *Molinia* meadow and the *Calluna/Empetrum* heathland sites were very different both in vegetation structure and soil moisture; the *Erica* and *Molinia* sites were similar in soil moisture but different in vegetation structure, and the *Erica* and the *Calluna/Empetrum* sites were somewhat similar in vegetational structure (all dwarf shrubs) but different in soil moisture. Yet, all were quite similar in their spider fauna. We found relatively large differences between bare and vegetated habitats, probably because bare sandy areas are without vegetational structure and also microclimatically extreme. Several xerophilic spider species are specialists of this habitat type.

Temporal changes in the spider community composition were greater than differences between habitats. This was not due to any dramatic changes over the years in the composition of the spider communities, however, because even these changes were quite small. This is not only evident from the high similarities, but also from a consideration of the specific changes. For example, the most abundant species that disappeared had a dominance score of only 2.2% at the site of highest abundance (*Arctosa perita* at traps 1–2). The appearing species that became most abundant reached a dominance score of 2.4% (*Macrargus carpenteri* at traps 5–6). Among the dominants the greatest difference in dominance score between 1977–79 and 1997–98 (all sites combined) was <5%. Thus, viewed over the 20 years, the composition of the spider fauna has been very stable. On a still longer time scale these communities will certainly not be maintained; most likely the area will be invaded by shrubs (a process already started) and eventually trees, and thus the vegetation

type will change completely, unless maintained by management. This development is accelerated by the planting of the forest that surrounds the heathland area, creating a much milder microclimate than before and providing invasive tree species.

The reasons for the temporal changes should be considered. For trap-sites 1–2, vegetational succession following a disturbance is the obvious cause. For the remaining sites the question is more difficult. We could see no pattern in the ecological preferences of species that decreased/disappeared or appeared/increased. The weather in 1997–98 was slightly warmer and dryer than before, but it is difficult to relate the specific faunistic changes to this fact, since the differences between the two early periods are as large as between early and late periods.

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APPENDIX 1

Nomenclature, name abbreviations and number codes for species mentioned in text and figures.

Ael.vin	<i>Aelurillus v-insignitus</i> (Clerck)
Arc.per	<i>Arctosa perita</i> (Latr.)
Agr.pro	<i>Agroeca proxima</i> (O.P.-C.) (16)
Alo.pul	<i>Alopecosa pulverulenta</i> (Clerck)
Bat.gra	<i>Bathyphantes gracilis</i> (Bl.)
Bol.lut	<i>Bolyphantes luteolus</i> (Bl.)
Cen.con	<i>Centromerita concinna</i> (Thor.) (3)
Che.err	<i>Cheiracanthium erraticum</i> (Walck.)
Che.vir	<i>Cheiracanthium virescens</i> (Sund.)
Clu.tri	<i>Clubiona trivialis</i> C.L.K.
Dra.cup	<i>Drassodes cupreus</i> (Bl.) (18)
Dra.pus	<i>Drasyllus pusillus</i> (C.L.K.) (19)
Euo.fro	<i>Euophrys frontalis</i> (Walck.)
Eva.mer	<i>Evansia merens</i> O.P.-C.
Gna.lep	<i>Gnaphosa leporina</i> (L.K.) (20)
Gon.rub	<i>Gonatium rubens</i> (Bl.) (4)
Gon.viv	<i>Gongylidiellum vivum</i> (O.P.-C.)
Hap.sig	<i>Haplodrassus signifer</i> (C.L.K.) (21)
Lep.eri	<i>Lepthyphantes ericaeus</i> (Bl.) (5)
Lep.men	<i>Lepthyphantes mengei</i> Kulcz. (6)
Lin.tri	<i>Linyphia triangularis</i> (Clerck)
Mac.car	<i>Macrargus carpenteri</i> (O.P.-C.) (7)
Mac.ruf	<i>Macrargus rufus</i> (Wider)
Mei.bea	<i>Meioneta beata</i> (O.P.-C.)
Mei.rur	<i>Meioneta rurestris</i> (C.L.K.)
Par.mon	<i>Pardosa monticola</i> (Clerck)
Par.nig	<i>Pardosa nigriceps</i> (Thor.) (13)
Par.pul	<i>Pardosa pullata</i> (Clerck) (14)
Pep.lud	<i>Peponecranium ludicrum</i> (O.P.-C.) (8)
Phi.his	<i>Philodromus histrio</i> (Latr.)
Pho.gib	<i>Pholcomma gibbum</i> (Westr.) (1)
Rob.liv	<i>Robertus lividus</i> (Bl.) (2)
Saa.abn	<i>Saaristoa abnormis</i> (Bl.)
Sco.gra	<i>Scotina gracilipes</i> (Bl.) (17)
Tro.ter	<i>Trochosa terricola</i> Thor. (15)
Typ.dig	<i>Typhocrestus digitatus</i> (O.P.-C.)
Wal.ant	<i>Walckenaeria antica</i> (Wider)
Wal.mon	<i>Walckenaeria monoceros</i> (Wider) (10)
Wal.nud	<i>Walckenaeria nudipalpis</i> (Westr.)
Wal.uni	<i>Walckenaeria unicornis</i> O.P.-C.
Zel.ele	<i>Zelotes electus</i> (C.L.K.)
Zel.lat	<i>Zelotes latreillei</i> (Simon) (22)
Zor.spi	<i>Zora spinimana</i> (Sund.) (23)

HABITAT DISTRIBUTION, LIFE HISTORY AND BEHAVIOR OF *TETRAGNATHA* SPIDER SPECIES IN THE GREAT SMOKY MOUNTAINS NATIONAL PARK

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ABSTRACT. Habitat distribution patterns of five species of *Tetragnatha* Latreille 1804 were studied by analyzing 1163 one-hour samples collected at 17 focal sites representing 16 major biotic communities (habitats) in the Great Smoky Mountains National Park. *Tetragnatha versicolor* Walckenaer 1841 is a habitat generalist, being common over a wide range of elevations (520–1755 m) and in 10 of the 16 habitats, including seven forest habitats as well as wetland, high grass bald, and grassland habitats. *Tetragnatha laboriosa* Hentz 1850 is virtually restricted to non-wetland grassy habitats, *T. elongata* Walckenaer 1805 to streams, *T. viridis* Walckenaer 1841 to hemlock trees, and *T. straminea* Emerton 1884 to non-forested wetlands (marshes). Microhabitat segregation exists in the high grass bald community between *T. versicolor* (prefers trees and shrubs) and *T. laboriosa* (prefers herbs). Size frequency histograms of seasonal samples of *T. straminea* specimens indicate that this species has a one-year life cycle with six post-emergent instars, and that most individuals overwinter in the antepenultimate instar and mature and mate in May and June. *Tetragnatha straminea* is able to capture prey with or without using a web and adopts stick-like cryptic postures in three different contexts.

Keywords: *Tetragnatha*, spider, habitat preference, life cycle, cryptic behavior

Being highly diverse and abundant predators, spiders are important regulators of terrestrial arthropod populations (Riechert & Bishop 1990; Coddington & Levi 1991; Moran et al. 1996) and may prove to be useful indicators of the overall species richness and health of terrestrial communities (Noss 1990; Kremen et al. 1993; Colwell & Coddington 1994; Hänggi et al. 1995). But progress toward understanding the ecological roles of spiders is limited by a lack of knowledge of the habitat preferences and life histories of many species (Duffy 1978; Hänggi et al. 1995). Ecologists must know the autecology and life histories of important constituent species before they can gain key insights into food web dynamics and other aspects of a community's dynamics (Olive 1980; Strong et al. 1984; Wilson 1992; Polis et al. 1996).

Tetragnatha Latreille 1804 may be the most widespread and abundant orb-weaving spider genus in the world (Levi 1981). *Tetragnatha* species live in tropical, temperate, and arctic climates and on all continents (except Antarctica) and many islands. On the Hawaiian Islands a major adaptive radiation of *Tetragnatha* species has been discovered (Gillespie

& Croom 1995). Fifteen *Tetragnatha* species are known from North America north of Mexico (Levi 1981), and some of these are numerically dominant spiders in particular habitats and over whole regions (Lowrie 1953; LeSar & Unzicker 1978). Despite the prominence of this genus, the life histories of only one North American species (*T. laboriosa* Hentz 1850) and a few species in other parts of the world have been rigorously analyzed and described (Juberthie 1954; Toft 1976; LeSar & Unzicker 1978), and knowledge of the habitat preferences of North American *Tetragnatha* species consists of collecting records and comments scattered widely in the literature.

In this study, we describe the habitat distribution patterns of five *Tetragnatha* species found in the Great Smoky Mountains National Park Biosphere Reserve (GSMNP) by using large sets of spider samples collected from 16 major habitats with a standardized protocol used to inventory the spiders of the GSMNP. Located in the southern Appalachian Mountains, the GSMNP, due partly to its wide elevation range (275–2013 m), large size (207,000 ha), and low temperate latitude

(35°35'N), comprises a rich mosaic of biotic communities appropriate for investigating habitat preferences on a landscape scale. We also provide the first analysis and description of the life history, phenology, and behavior of *Tetragnatha straminea* Emerton 1884. Our main goal is to make this important assemblage of spiders more accessible to ecologists.

METHODS

Habitat distribution.—Teams of 3–5 (usually 4) collectors used a modified Coddington sampling protocol (Coddington et al. 1996) to obtain the 1163 one-hour ground (408), aerial (310), beat (360), and sweep (85) samples of spiders used in this project. Ground sampling involved searching below knee level mostly on hands and knees, exploring leaf litter, logs, rocks, and plant surfaces. Aerial sampling involved searching foliage, branches, tree trunks, and spaces in between, from knee height up to maximum overhead arm's reach. Beating consisted of striking vegetation with a 1 m long stick and dislodging spiders onto a 0.5 m² canvas sheet held horizontally below the vegetation. Hands and aspirators were used to collect the spiders into vials containing 80% ethanol. One sample unit equaled one hour of uninterrupted effort using one of these three methods during which the collector attempted to collect every spider encountered. During each hour the team as a whole typically used all three methods in the same area. In non-forest communities (grass bald, wetland, and native grassland sites) one-hour sweep sampling was substituted for aerial and/or beating methods; sturdy sweep nets with 38 cm diameter hoops were used, and the number of sweeps per hour (175–400, mean and SD = 268 ± 48) depended primarily on vegetation structure and spider abundance.

Two sets of samples (one in the spring and one in late summer) were collected in each of two years (1996 and 1997) from 15 sites and in 1995 from two other sites, the low grass bald and heath bald sites. These 17 focal sites were selected by GSMNP ecologists to represent the 16 major habitat (community) types found in the GSMNP. Habitat type, locality data, collecting dates, and sampling effort for each focal site are given in the Appendix. Two montane wetland focal sites were chosen because each one was too small to support the sampling effort judged necessary for this

study. For a given focal site, the number of samples collected in the spring and summer were equal or very nearly so, as were the number of samples collected in 1996 and 1997. At each site (with the exception of the high grass bald and both montane wetland sites) nearly equal numbers of samples were collected with each of the methods employed. Descriptions of most of the sampled community types can be found in Whittaker (1956). Vegetation is being analyzed at each focal site by GSMNP botanists, and the results of these analyses will be posted in one or two years on the World Wide Web.

Adult and juvenile *Tetragnatha* specimens were sorted from each sample and identified to species. By using eye arrangement, pigment pattern, and abdominal shape, we were able to identify all but about 1% of the juveniles. *Tetragnatha versicolor* Walckenaer 1841 and *T. laboriosa* juveniles cannot be separated by eye and body shape characters, but can be distinguished by the following: in *versicolor* the black pigment area surrounding each lateral eye touches that of its neighboring lateral eye (clearly separate in *laboriosa* except in some of the youngest individuals), the abdominal venter is light (dark in *laboriosa*), and the silver pigment dorsally on the abdomen of the smallest specimens is often interrupted by a median dorsal line of no pigment (not interrupted in *laboriosa*). All specimens will be deposited in the Smithsonian Institution.

The relative abundance (mean number of individuals per one-hour sample) of each species in each year was computed for each of the 17 sites. It is important to note that this index of abundance does not reveal the often wide variation in number of individuals among one-hour samples at each site, variation due largely to method bias to particular microhabitats, spatial environmental variation within each site, and seasonal changes in spider abundance correlated with species' phenologies. An ANOVA (StatView 4.5 from Abacus Concepts) was used to examine the effect of year and method on spider abundance; $P < 0.05$ was our significance criterion.

Life history.—We measured the length of the left tibia I (ITL) (along the dorsal surface) of all 220 *T. straminea* specimens collected at the two montane wetland sites, Meadow Branch marsh (15 May and 17 July 1996; 23

May, 1 August, and 7 October 1997) and Indian Creek marsh (27 May and 16 August 1996; 12 May and 29 July 1997). Toft (1976) demonstrated that ITL often distinguishes spider instars more clearly than does either the length or width of the carapace. Measurements were performed with a Wild M-5 stereomicroscope at 24 \times and 12 \times magnification and are accurate to ± 0.077 mm. We used the StatView 4.5 computer program to generate ITL frequency distribution histograms. By examining these histograms of seasonal subsets (spring, summer, and fall) of data pooled from both sites, it was possible to reveal phenology (seasonal timing of development) and generation time (life cycle length). The histogram for all data pooled revealed the total number of instars.

Behavior.—We observed and photographed live specimens in the field. Several *T. straminea* juveniles (antepenultimate instar) were placed in separate terraria and maintained for several weeks on *Drosophila* flies while we observed prey capture and cryptic postures, sometimes using a hand-held magnifier.

RESULTS

Habitat distribution.—Five species of *Tetragnatha* were collected in the GSMNP: *T. elongata* Walckenaer 1805, *T. laboriosa*, *T. straminea*, *T. versicolor*, and *T. viridis* Walckenaer 1841. Table 1 and Fig. 1 show the relative abundance of these species at each focal site. *Tetragnatha versicolor* was found at 16 of the 17 focal sites and was common (relative abundance = 0.5–2.0) or abundant (relative abundance > 2.0) in 10 of the 16 habitats, including seven forest habitats as well as montane wetland, high grass bald, and native grassland habitats. It was especially abundant in mixed oak forest. *Tetragnatha laboriosa* was found at nine sites, but was rare at all but two of these sites, native grassland and high grass bald. *Tetragnatha versicolor* and *T. laboriosa* were found over a wide elevational range (520–1830 m). *Tetragnatha straminea* was collected at only three sites, the montane wetland and native grassland sites, and was common or abundant at all three. *Tetragnatha elongata* was found only at the two sites through which streams flow. *Tetragnatha viridis* was found only at the two sites where hemlock trees are abundant.

No *Tetragnatha* species were common at the spruce-fir, spruce, northern hardwood, low grass bald, or heath bald sites, and none were collected at the pine-oak (395 m) site (Table 1, Fig. 1). Sites with two or more common species of *Tetragnatha* were the high grass bald (*versicolor* and *laboriosa*), both wetlands (*versicolor* and *straminea*), and the native grassland (*versicolor*, *laboriosa*, and *straminea*) (Fig. 1).

There were significant relative abundance differences between 1996 and 1997 for *T. versicolor* at the mixed oak, Table Mountain pine, hemlock/hardwood cove, hardwood cove, and Meadow Branch wetland sites, and for *T. laboriosa* at the native grassland (Fig. 1). In each case, the relative abundance was higher in 1997.

Microhabitat distribution.—At the high grass bald, *T. laboriosa* was more abundant in sweep samples (collected from herbaceous vegetation) than in beat samples (collected from shrubs and trees) ($F = 5.64$, $df = 1$, $P = 0.025$), whereas *T. versicolor* was more abundant in beat than in sweep samples ($F = 5.64$, $df = 1$, $P = 0.025$) (Fig. 2). At the Indian Creek wetland site, *T. straminea* was more abundant in sweep samples than in beat samples ($F = 5.17$, $df = 1$, $P = 0.041$), but *T. versicolor* was equally common in both sweep and beat samples ($F = 0.24$, $df = 1$, $P = 0.632$) (Fig. 3). Although we were unable to make this kind of microhabitat comparison at the Meadow Branch wetland or native grassland sites (because the beat method was not used at these sites), we observed that *T. straminea* was more common in the low grassy vegetation of the wetter parts of these habitats than was *T. versicolor*. The few specimens of *T. viridis* that were found were collected only by beating the foliage of hemlock trees. *Tetragnatha elongata* was collected only over the small streams flowing through the hemlock and native grassland sites.

Life history of *T. straminea*.—The size frequency histogram of all *T. straminea* individuals collected at the wetland sites during both years indicates a total of six size/age classes and, therefore, six post-emergent instars (instars living outside the egg sac) (Fig. 4). As is typical for spiders (Toft 1976; Coyle 1985) the older the instar, the greater the variation in size. For two reasons, we suspect that the ITL frequency peak between 4.5 and 5.0

Table 1.—Relative abundance of *Tetragnatha* species at 17 focal sites representing 16 biotic communities in the Great Smoky Mountains National Park in both 1996 and 1997 (1996 and 1997 values are separated by a comma). Low grass and heath balds were sampled in 1995 only. Elevation (m) of each site is given in parentheses. Relative abundance value is underlined if at least one adult was collected.

Habitat/focal site	Relative abundance (mean number of individuals per sample)				
	<i>elongata</i>	<i>laboriosa</i>	<i>straminea</i>	<i>versicolor</i>	<i>viridis</i>
Spruce-fir (1830)		0, 0.04		0, 0.08	
High grass bald (1755)		0.88, <u>1.67</u>		1.46, 2.25	
Spruce (1715)		0, 0.08		0.13, 0.04	
Beech gap (1645)				<u>0.50</u> , 0.21	
Northern hardwood (1615)				<u>0.16</u> , <u>0.30</u>	
Red oak (1555)				<u>0.40</u> , <u>1.08</u>	
Low grass bald (1505)		<u>0.17</u>		0.40	
Heath bald (1390)				0.10	
Mixed oak (1115)				<u>5.82</u> , <u>18.0</u>	
Table Mtn. pine (1005)		0.02, 0		0.06, 0.58	
Hemlock-hardwood cove (945)				<u>1.15</u> , <u>2.75</u>	<u>0.04</u> , <u>0.06</u>
Hemlock (885)	<u>0.17</u> , <u>0.19</u>			<u>1.73</u> , <u>3.36</u>	<u>0.02</u> , <u>0.03</u>
Hardwood cove (740)		0, 0.02		<u>0.43</u> , <u>1.25</u>	
Wetland (Indian Cr.) (685)		<u>0.06</u> , 0	<u>2.00</u> , <u>3.31</u>	<u>0.24</u> , <u>1.38</u>	
Wetland (Meadow Br.) (535)		0, <u>0.19</u>	<u>2.00</u> , <u>3.94</u>	<u>0.24</u> , <u>3.31</u>	
Native grassland (520)	0, <u>0.13</u>	<u>0.13</u> , <u>2.17</u>	<u>0.08</u> , <u>0.80</u>	<u>0.04</u> , <u>0.54</u>	
Pine-oak (395)					

mm does not represent the modal value of one instar with a very broad size range, but is instead the result of size overlap between post-emergent instars IV and V: 1) The size range of adult females should be greater than that of any younger instar. 2) The ITL range of the penultimate male cohort (recognized by swollen palpal tarsi) should approximate that of the penultimate females. Adult females were distinguished by their protuberant genital area (and by fully developed spermathecae whenever dissections were performed). Penultimate females (instar V) were distinguished on the basis of size and the absence of a protuberant genital area. Size frequency histograms of seasonal subsets of *T. straminea* specimens collected at both wetland sites show in late spring (12–27 May) adult and penultimate males, adult and penultimate females, and relatively large juveniles, most of which are presumably antepenultimate (Fig. 5). The summer (17 July–16 August) sample set contained a smaller number of adult females and younger juveniles (instars I–III) than were present in the spring. The fall (7 October) sample set (from Meadow Branch wetland) was composed only of a juvenile class (instars III–IV) with a mean ITL between that of the spring and summer

samples. These seasonal patterns strongly support a life history pattern of one generation per year with most individuals overwintering in the antepenultimate instar. Males and females appear to mature and mate in May and June. Many adult females persist well into the summer months, but males are absent then, suggesting that they die soon after mating.

Behavior of *T. straminea*.—In the field, the orientation of *T. straminea* orbs varied from horizontal to diagonal. Some spiders were in the center of their web adopting a roughly stick-like posture (legs I and II extended forward fairly close to one another and legs III and IV extended backward near the sides of the abdomen). Others were stretched out on a twig or grass blade with legs I and II held together, the much shorter legs III surrounding and gripping the substrate, and legs IV extended backward along the sides of the abdomen. This second posture, in concert with the slender abdomen and pale yellow-brown color, made the spider exceedingly difficult for us to locate. Sometimes we could not find the captive spiders that had adopted this very cryptic posture without jarring the dead grass stems in their containers. When disturbed in this way, the spider would sometimes drop

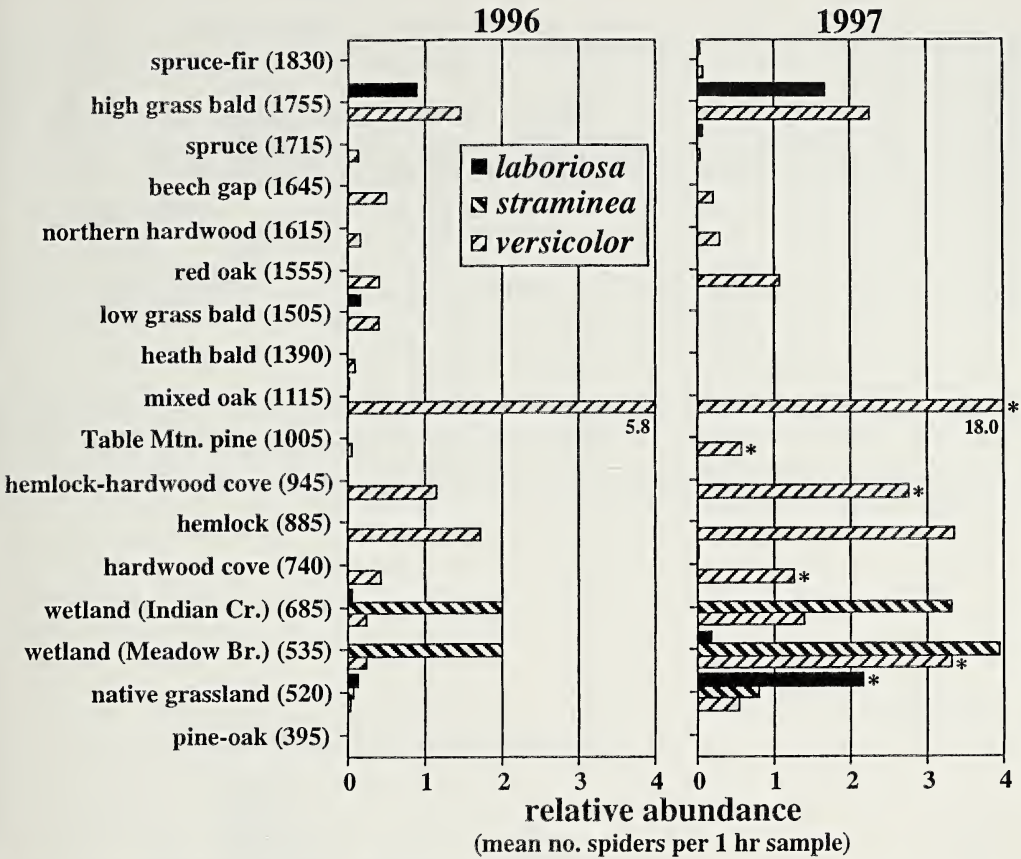


Figure 1.—Relative abundance of the three most common *Tetragnatha* species in 1996 and 1997 at 17 focal sites representing 16 biotic communities in the Great Smoky Mountains National Park. Low grass and heath bald sites were sampled in 1995 only. Focal sites are listed in order from lowest to highest elevation (in meters within parentheses). An asterisk marks any bar representing a relative abundance value significantly higher than one for the same species and site in the other year (ANOVA, $P < 0.05$).

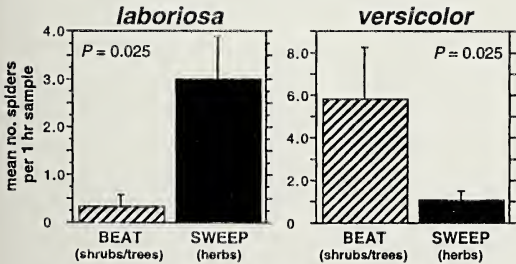


Figure 2.—Microhabitat distribution of *Tetragnatha* species at the high grass bald site. $n = 12$ beat and 18 sweep samples. Standard error is shown on top of each bar. The P -value is generated by ANOVA; see text for test statistics.

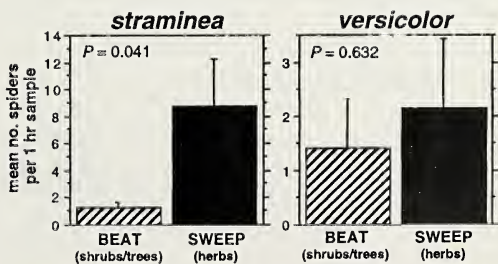


Figure 3.—Microhabitat distribution of *Tetragnatha* species at the Indian Creek wetland. $n = 8$ beat and 7 sweep samples. Standard error is shown on top of each bar. The P -value is generated by ANOVA; see text for test statistics.

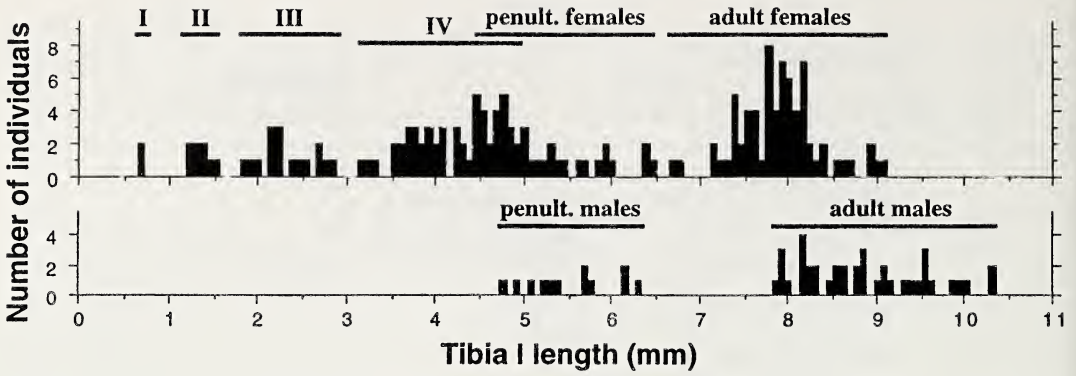


Figure 4.—Size (ITL) frequency distribution histograms of all 220 *Tetragnatha straminea* individuals collected at the two montane wetland sites during 1996 and 1997. Females and individuals too young to be sexed are graphed separately from penultimate and adult males. Labeled horizontal bars indicate ITL ranges of putative and known (adults and penultimate males) post-emergent instars.

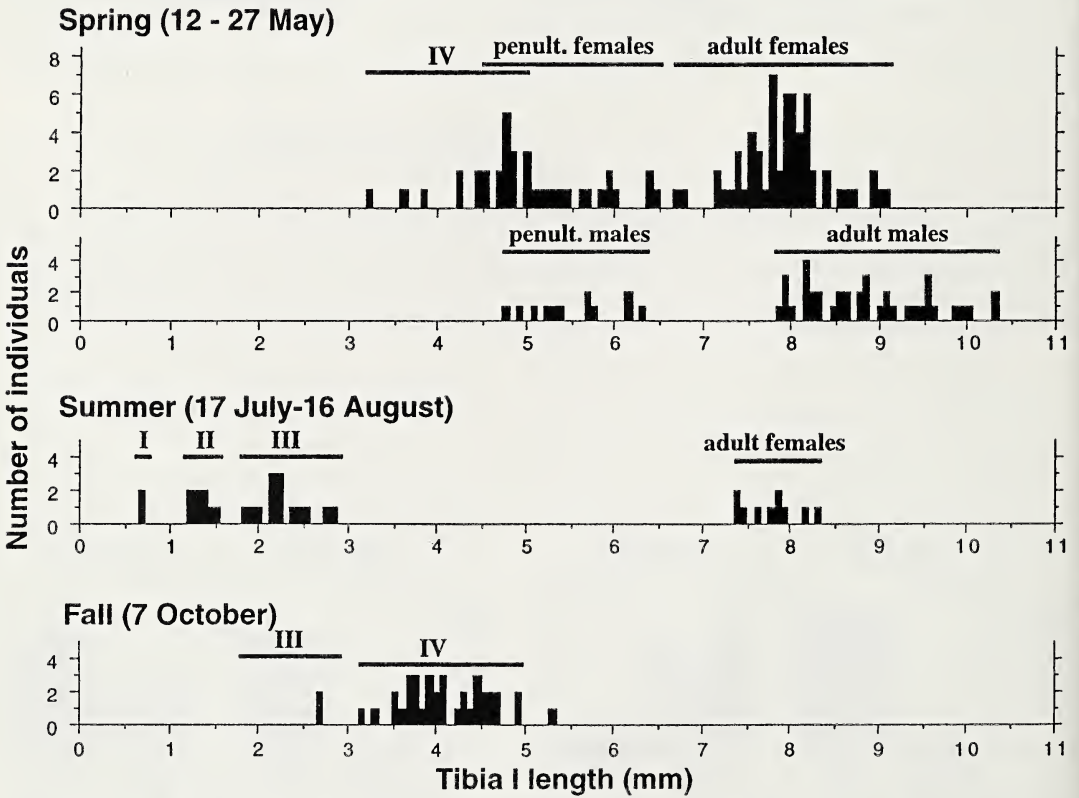


Figure 5.—Size (ITL) frequency distribution histograms of seasonal subsets of all 220 *Tetragnatha straminea* individuals collected at the two montane wetland sites during 1996 and 1997. Females and individuals too young to be sexed are graphed separately from penultimate and adult males. Labeled horizontal bars indicate ITL ranges of putative and known (adults and penultimate males) postemergent instars.

and assume this cryptic stick-like posture while hanging suspended in mid-air from its dragline.

Twice we were able to directly observe these spiders capture *Drosophila* flies without using a web. In the first observation, the fly was walking on the twig under which the spider was positioned cryptically. The fly appeared to hit one of the spider's third legs (which were wrapped around the twig) and it was seized instantly. In the second observation, the spider was ascending the side of its glass cage when a fly walked into it. The spider's first two pairs of legs instantly surrounded the fly for a brief moment until the spider could grasp it with its chelicerae. Silk was not used to immobilize either of these flies. Following these and other less closely observed capture attempts not involving webs, the spider crushed and manipulated the prey with its chelicerae and pedipalps. We often observed individuals holding in their chelicerae 1–5 flies which had been captured without a web. Occasionally, such spiders with two or more flies in their mouthparts would capture additional live flies (that we held in contact with the web) by grabbing them with the first legs and immediately wrapping them in silk with the hind legs. These immobilized flies were left attached to the web, and since we could not find them on the following day, we presume they were eaten.

DISCUSSION

Habitat and microhabitat distribution.—

Clearly, *T. versicolor* is a habitat generalist. Our finding that it is common or abundant over a wide elevation range in a wide variety of forest communities as well as wetland, grass bald, and grassland habitats, is consistent with collection records cited by Levi (1981). Although it appears to prefer woody vegetation and can thrive in dryer situations than many of its congeners, it can also be found on herbaceous vegetation in marshy areas. Our observations, which are consistent with those of Comstock (1912), Lowrie (1953), Levi (1981), and Kaston (1981), show that *T. laboriosa*, like *T. versicolor*, often lives far from aquatic habitats, but, unlike *T. versicolor*, rarely occurs in forests and is virtually restricted to non-wetland grassy habitats. In spite of this restriction, it thrives over a wide range of natural and agricultural communities

and elevations (Levi 1981) and is the most abundant spider in New York alfalfa fields (Wheeler 1973) and central Illinois soybean fields (LeSar & Unzicker 1978). We suspect that the very few individuals of *T. laboriosa* collected at forest sites within the GSMNP were immigrants that had ballooned from non-forest habitats and would not have matured and reproduced where we found them; this view is supported by LeSar & Unzicker's (1978) observations that early instars of *T. laboriosa* are good ballooners and colonizers and by the fact that every forest-dwelling individual we collected was an early instar juvenile.

Our data indicate that *T. straminea*, *T. viridis*, and *T. elongata* are all habitat specialists. The restriction of *T. straminea* to non-forested wetlands in the GSMNP is consistent with collection records cited by Levi (1981). Levi's (1981) observation that *T. viridis* is restricted to conifers matches our findings. We suspect that our data underestimates the abundance of *T. viridis* at the two sites where we found it because 1) it may frequent the large volume of hemlock canopy foliage above our sampling zone, 2) its green color and abandonment of web-building make it difficult to locate visually, and 3) it may be especially difficult to dislodge (Levi 1981). Our observation that *T. elongata* is strictly riparian and nearly always builds its webs over open water match those of Lowrie (1953), Levi (1981), Kaston (1981), and Gillespie (1987). According to the distribution records in Levi (1981), there are only two other species of *Tetragnatha* that we think might eventually be found in the GSMNP, *T. guatemalensis* O.P.-Cambridge 1889 and *T. pallescens* F.P. Cambridge 1903. If these two are living in the GSMNP, they are not common.

The finding that *T. versicolor* is distributed among more habitats in the GSMNP and elsewhere than are *T. straminea*, *T. viridis*, and *T. elongata*, and the observation that this species has a higher (67°N) and larger (54') latitudinal and geographic (ca. 20.7 billion km²) range than the other three species (46–57°N; 16–34'; 1.6–7.8 billion km²) (Levi 1981), appear to fit a taxonomically widespread biodiversity pattern where habitat generalists in many taxa tend to occupy broader latitudinal and geographical ranges than do habitat specialists (Stevens 1989; Wilson 1992). However, *T. la-*

boriosa, which appears from our data to be less of a habitat generalist than *T. versicolor*, has much the same geographic range as *versicolor*. Apparently, the ability of *T. laboriosa* to colonize and reproduce in open habitats suits it well to utilizing a wide array of edaphic and early successional non-forest habitats which have proliferated because of increased human impact on landscapes and which are simply not well represented in the GSMNP. In other words, its status as a habitat generalist cannot be fully expressed in the GSMNP landscape.

Our results indicate that the coexistence of *T. versicolor* and *T. laboriosa* at the high grass bald site involves microhabitat segregation in a patchy community; *versicolor* lives primarily in the shrubs and small trees that are scattered within and surround the open areas of grass and other herbs where *laboriosa* lives. It is puzzling why no adults of *T. versicolor* were collected here despite the abundance of juveniles (Table 1). Perhaps this population is largely or wholly maintained by aerial immigration from high density forest-dwelling populations at lower elevations; this hypothesis remains to be tested. The beat vs. sweep data from the Indian Creek wetland site suggest that the *T. versicolor* population there is not as distinctly segregated from the *straminea* population. However, observations during an autumn sampling effort in the Meadow Branch wetland, as well as *T. versicolor*'s ability to prosper away from aquatic habitats, suggest to us that an appropriate sampling design would reveal that the *straminea* population is concentrated in grasses and other herbs in the wetter part of these wetlands while the *versicolor* population is chiefly found on taller and more sturdy vegetation in the dryer areas.

The significantly higher relative abundance values in 1997 as compared to 1996 for *T. versicolor* at several sites and for *T. laboriosa* at one site may be the result of population increases. However, we suspect that the 1997 sampling team devoted more effort to collecting small juveniles (particularly from beating sheets and sweep nets) than did the 1996 team, thus creating a bias which might have caused these relative abundance differences.

Life history.—Ours is the first life history analysis of *T. straminea*. This and other life history analyses of north temperate *Tetragnatha* species show that one-year life cycles

may be the rule in this genus; Finnish populations of *T. extensa* (Linnaeus 1758), *T. obtusa* C.L. Koch 1837, and *T. montana* Simon 1874, and Illinois populations of *T. laboriosa* all have annual cycles (Toft 1976; LeSar & Unzicker 1978). Much like *T. straminea*, these species overwinter in mid-to-late juvenile instars and mature and mate in late spring or early summer. However, Juberthie (1954) showed that in southern France *Tetragnatha* species may have two generations per year. LeSar & Unzicker (1978) found that lab-reared *T. laboriosa* has eight postemergent instars, rather than the six our field data indicate for *T. straminea*, but the natural phenologies of these two species are very similar.

Behavior.—The cryptic, stretched-out stick-like postures of *T. straminea* (on its web, on vegetation, or hanging in mid-air), like similar postures adopted by other species of *Tetragnatha* and unrelated spiders like *Deinopis* MacLeay 1839 (Comstock 1912; Bristowe 1958; McKeown 1963; Forster & Forster 1973; Levi 1981; Kaston 1981; Gillespie & Croom 1995; Getty & Coyle 1996), surely must serve to reduce an individual's chances of being detected or recognized as prey by visual predators. The remarkably flexible prey capture behavior we have observed in *T. straminea*—the ability to catch prey both with and without the use of a web—has also been observed by Luczak & Dabrowska-Prot (1966) in a Eurasian species, *T. montana*. This versatile capture program, which may be more widespread in the genus than is currently appreciated, may help explain the origin of non-web-building cursorial spiny-legged lineages represented by *T. viridis* (Levi 1981) and several Hawaiian species (Gillespie & Croom 1995).

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APPENDIX

Habitat type, locality data, collecting dates, and sampling effort for each of the 17 focal sites (listed in order from highest to lowest elevation). Number of ground, aerial, beat, and sweep samples given in parentheses after total number of one-hour samples.

Spruce-fir forest: NORTH CAROLINA: *Swain County*, 0.5 km SW Mt. Collins, N & S sides of Appalachian Trail, E2755, N39403, 1815–1845 m elev., 26 June 1996, 14 September 1996, 11 June 1997, 23 August 1997. 48 samples (16–16–16–0).

High grass bald: NORTH CAROLINA: *Swain County*, Andrews Bald, E2738, N39354, 1755 m elev., 27 June 1996, 22 September 1996, 12 June 1997, 6 September 1997. 48 samples (18–0–12–18).

Spruce forest: NORTH CAROLINA: *Swain County*, just SW junction of Noland Divide Trail and road to pumping station, E2755, N39382, 1715 m elev., 20 June 1996, 7 September 1996, 10 June 1997, 23 August 1997. 48 samples (16–16–16–0).

Beech gap forest: NORTH CAROLINA: *Swain County*, in hog enclosure below Appalachian Trail at 350 m E Road Prong Trailhead, E2786, N39433, 1645 m elev., 14 June 1996, 15 August 1996, 10 June 1997, 13 August 1997. 48 samples (16–16–16–0).

Northern hardwood forest: NORTH CAROLINA: *Haywood County*, Cataloochee Divide just above Hemphill Bald Trail at 200 m E Garrett's Gap, E3055, N39359, 1615 m elev., 12 and 15 June 1996, 14 August 1996, 6 June 1997, 12 August 1997. 84 samples (29–27–28–0).

Red oak forest: NORTH CAROLINA: *Swain County*, Roundtop Knob, E of Noland Divide Trail about 2 mi SE Clingman's Dome Road, E2770, N39364, 1555 m elev., 24 June 1996, 31 August 1996, 4 June 1997, 11 August 1997. 88 samples (30–28–30–0).

Low grass bald: NORTH CAROLINA: *Swain County*, Gregory Bald, E2401, N39343, 1505 m elev., 3–5 June 1995, 29–30 September 1995. 72 samples (24–0–24–24).

Heath bald: TENNESSEE: *Sevier County*, Inspiration Point on Alum Cave Trail, E2789, N39461, 1390 m elev., 25–25 May 1995, 23–24 September 1995. 72 samples (24–24–24–0).

Mixed oak forest: TENNESSEE: *Sevier County*, E, S, & W slopes of Chiquapin Knob, E2639, N39512, 1083–1144 m elev., 13 June 1996, 13 August 1996, 2 June 1997, 7 August 1997. 85 samples (29–26–30–0).

Table Mountain pine forest: TENNESSEE: *Sevier County*, about 200 m N of route 441 loop NW of Chimneys picnic area, E2738, N39471, 976–1037 m elev., 6 June 1996, 6 August 1996, 27 May 1997, 6 August 1997. 64 samples (23–18–23–0).

Hemlock-hardwood cove forest: TENNESSEE: *Sevier County*, N & E Grotto Falls Trailhead at Roaring Fork Motor Trail, P. White veg. plot, E2772, N39512, 945 m elev., 22 May 1996, 30 July and 1 August 1996, 19 May 1997, 4 August 1997. 96 samples (32–32–32–0).

Hemlock forest: NORTH CAROLINA: *Haywood County*, Cataloochee, 150 m S mouth of Palmer Branch at Caldwell Fork, E3107, N39436, 854–915 m elev., 4 June 1996, 5 August 1996, 18 May 1997, 1 June 1997, 10 and 24 August 1997. 84 samples (29–26–29–0).

Hardwood cove forest: TENNESSEE: *Sevier County*, along Porter's Creek Trail at 200 paces above bridge over Porter's Creek, E2830, N39508, 740 m elev., 18–19 June 1996, 24–25 August 1996, 21–22 May 1997, 31 July 1997. 116 samples (39–37–40–0).

Wetland (Indian Creek): NORTH CAROLINA: *Swain County*, marsh between Indian Creek Trail and Indian Creek at 2 mi. NE of junction with Deep Creek Trail, E2817, N39296, 685 m elev., 27 May 1996, 16 August 1996, 12 May 1997, 29 July 1997. 33 samples (14–4–8–7).

Wetland (Meadow Branch): TENNESSEE: *Blount County*, marsh along Meadow Branch at 0.5 km ENE of Dosey Gap, E2527, N39470, 535 m elev., 23 May 1996, 1 August 1996, 15 May 1997, 17 July 1997. 33 samples (13–8–0–12).

Native grassland: TENNESSEE: *Blount County*, Cades Cove, S side Abrams Creek about 0.3 mi. upstream from Cades Cove Loop Road bridge, E2426, N39423, 520 m elev., 5 June 1996, 8 August 1996, 15 May 1997, 17 July 1997. 48 samples (24–0–0–24).

Pine-oak forest: TENNESSEE: *Blount County*, 300 m N of junction of Tabcat Creek and Maynard Creek, E2301, N39347, 395 m elev., 28–29 May 1996, 2 August 1996, 14 May 1997, 15 July 1997. 96 samples (32–32–32–0).

SPIDER BIODIVERSITY IN CONNECTION WITH THE VEGETATION STRUCTURE AND THE FOLIAGE ORIENTATION OF HEDGES

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ABSTRACT. The relationship between the structure of spider communities and an index of hedge ecological quality (based on an analysis of vegetation architecture using vegetation diversity and foliage cover) was investigated. The comparison deals with six hedges each of low, medium and high ecological value. The species richness and species composition of dominant spiders was the same for hedges of different quality. Thus it is concluded that these two simple parameters cannot reflect the diversity of the hedge foliage. Indicating species of the differences between ecological quality of two hedges could be required among the groups of species absent from one type of hedge. However, the foliage orientation of the hedges may induce substitution of spider species; thus special attention must be paid to the foliage orientation when comparing the spider communities inhabiting the hedges.

Keywords: Foliage cover, foliage orientation, species richness

Shrubby and raised hedges constitute one of the major elements supporting faunistic diversity within rural landscapes. In western France in particular, studies undertaken on woody areas have shown the close associations between the vegetation architecture of the hedges and the diversity or density of the hedge-inhabiting fauna, especially birds, small mammals, reptiles and insects (Saint Girons 1994; Constant & Eybert 1995; Burel 1996). On a regional scale, classifications, based on vegetation, have been established to define the suitability of hedges for certain fauna, such as game birds (Brown & Aubineau 1989). To achieve the goals of hedgerow management (maintenance of biodiversity, wood production, amelioration of climatic effects and improvement of water quality), a special index of classification for the ecological value of the hedges was developed by Rozé (1995). This index was based on an analysis of the major architectural characteristics of hedges (vegetation diversity and percentage of foliage cover). Numerous workers have detailed the strong relationship between vegetation structure and the composition of spider communities; and it is often argued that this is the most important parameter involved in web site selection (Wise 1993). Consequently, it is expected that the diversity of spiders and the

species composition of the dominant spiders in hedge foliage can reflect the hedge ecological value when that value is defined by an index of quality integrating the vegetation architecture. The aim of this work was to investigate the relationship between the variation in the ecological index proposed by Rozé (1995) and the variation in the associated spider communities. A comparison of the spider communities inhabiting hedges of different ecological values is presented.

METHODS

Study area and index of hedge quality.—The area investigated was situated in an agricultural landscape of Brittany (western France) consisting of fallow-fields (24.5 ha) surrounded by raised hedges for which density reached 1700m/10 ha. The plot was in the district of Candé-La Brocherie at 1°2'W, 47°34'N. The evaluation method used to assess hedge quality took into account the floristic composition and structure of the hedges (Rozé 1995; Table 1). A high biological value was allotted to the hedges when they were established on a complex of ditches or slopes, when the foliage cover of the shrubby and arborescent layers was high, and when brambles and nettles were wanting. Additional points were allotted when species, which were not very

Table 1.—Card-data for the evaluation of the biological quality of one hedge. The number of points is indicated in parentheses.

1) Slope/Ditch complex	
ditch	(1)
slope	(1)
double hedge	(1)
ditch elevation (>1 m)	(2)
2) Trees	
percentage of re-covering	
<20%	(0)
20 < % <50	(1)
>50%	(2)
spontaneous species (oak. . .)	(1)
not frequent species (alder, hornbeam. . .)	(1)
seedlings	(1)
3) Shrubs	
percentage of re-covering	
<20%	(0)
20 < % < 50	(1)
>50%	(2)
specific diversity 2–3 sp.	(1)
>4 sp.	(2)
original vegetation (spindle tree. . .)	(1)
4) Edge vegetation	
<i>Endymion non scripus</i> & <i>Anemone nemorsa</i>	(3)
<i>Umbilicus rupestris</i> & <i>Polypodium vulgare</i>	(2)
<i>Ruscus aculeatus</i> & <i>Rubis perenigra</i>	(2)
<i>Teucrium scorodonia</i> & <i>Stellaria holostea</i>	(1)
<i>Juncus effusus</i> + hydrophilous vegetation	(1)
<i>Rubus fruticosus</i> & <i>Dactylis glomerata</i>	(0)
<i>Pteridium aquilinum</i>	(0)
<i>Rubus fruticosus</i> & <i>Dactylis glomerata</i>	(0)
<i>Urtica dioica</i>	(–1)

frequently distributed at a regional scale, were present. The range of hedge ecological quality values varied from 1–20 which provided a comparative index for the biological quality of each hedge. **Collection of spiders and data analysis.**—Our previous investigations into the spider communities inhabiting shrub layers in western France have demonstrated that there was no considerable variation between the species composition of the “spring community” and the “annual community” for successive years (Canard 1979; Canard 1984; Ysnel et. al. 1996). These results concerning the temporal stability of the spider commu-

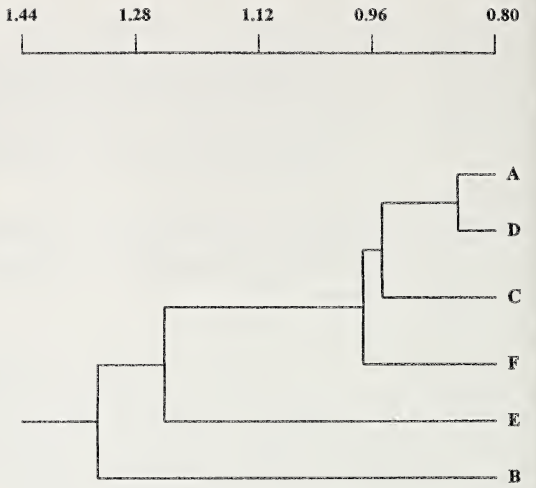


Figure 1.—Dendrogram of hedge similarity (UGPMA clustering method) concerning foliage spider communities.

nities justified our comparison here of different hedge communities during spring. Six hedges (A–F) were selected according to their index of biological quality to provide two hedges in each of three categories: hedge A (index of 20) and B (19) to “high”; hedge C (11) and D (9.5) to “medium”; and hedge E and F (6.5) to “low.” All the selected hedges were situated in a complex of three contiguous fallow-fields. The foliage spiders were collected by six series of branch-beating during spring 1997 (March, April, May) using a beating tray of 0.7 m² and a walking stick. Two people collected the spiders, one person was beating while another one was collecting the spiders from the tray with the aid of a pooter. Spiders were sampled over a total of 75 m for each hedge, which was comprised of 15 samples, with each sample of 5 linear meters at each of three heights: low (ground level), medium (at 1 m) and high (at 2 m). For each 5 meter sample at a given height, five tablecloths were placed on the ground and three whacks per tray were given to help achieve an “equal beating effort” across all samples. Since the beating method collects spiders only during their diurnal activity period (McCaffrey et. al. 1984), the timing of beating was randomly distributed across all hedges and heights sampled. This method obviously undersampled nocturnal spiders. To estimate the potential influence of foliage orientation, sampling was carried out along 20 m

Table 2.—Foliage spider communities and ecological value of hedges (ind/m: mean number of individuals per linear meter; sp/m: mean number of species per linear meter; J': Shannon evenness index).

Hedge quality	Specific diversity		sp/m ±SD	ind/m ±SD	J'	Foliage orientation
High	hedge A	47	2 ± 0.56	14.3 ± 2.7	0.68	NE
	hedge B	35	1.5 ± 0.35	6.2 ± 2.1	0.87	W
	Total specific diversity:	53				
Medium	hedge C	34	2.1 ± 0.34	11.3 ± 3.4	0.84	E
	hedge D	41	2.1 ± 0.30	9.7 ± 1.9	0.81	SE
	Total specific diversity:	46				
Low	hedge E	44	1.8 ± 0.73	6.6 ± 2.7	0.81	N
	hedge F	30	1.3 ± 0.22	5.2 ± 2.4	0.79	W
	Total specific diversity:	51				

of each side of hedge D during September 1997.

The nomenclature of spiders used follows Platnick (1997). The juveniles of the following genera were considered to belong to only one species: *Agroeca* sp, *Episinus* sp., *Zora* sp., *Pirata* sp., *Evarcha* sp., *Micaria* sp., *Cheiracanthium* sp., *Zelotes* sp., *Zygiella* sp., *Tibellus* sp., *Xysticus* sp.

Clubiona sp , *Heliophanus* sp, *Leptyphanes* sp. *Ozyptila* sp., *Robertus* sp. and *Tetragnatha* sp. were counted as species where there were only juveniles in what was collected. In order to simplify the comparison of the spider communities, the “dominant species” refers to species represented by at least 4.5% of the total individuals collected in one hedge.

A cluster analysis was performed by NTSYS-PC program with the use of the UGPMA method. The similarity matrices for community analyses were derived using the chi-squared distance by means of the following formula:

$$d_{ij} = \sqrt{\sum_k^p (x_{ki}/x_i - x_{kj})^2/xk}$$

An ANOVA (multiway factor analysis) was also performed by STATGRAPHIC-PC program to test the differences between the hedges. This analysis considered variation from two factors: hedge quality and number of individual per species. The variables examined were first transformed in percentages for the anova analysis and the data from couple of hedges of low, medium or high value were pooled.

RESULTS

Species richness and index of density.—A total of 72 genera and species was identified from the foliage of the six hedges studied (Appendix 1). The average species richness of the three categories of hedges remained virtually identical (Table 2), and a hedge of low ecological value could harbor a species richness greater than that in a hedge of high value.

Table 3.—Percentage of shared species between hedges (T = total number of species; s.s. = shared species).

	A-B	A-C	A-D	A-E	A-F	B-C	B-D	B-E	B-F
T	53	51	59	58	51	41	52	52	30
s.s.	24	27	29	25	21	22	26	22	20
%	45.2	53	49.1	43.1	41.2	53.7	50	42.3	66.7
	C-D	C-E	C-F	D-E	D-F	E-F			
T	46	43	40	58	50	48			
s.s.	25	27	23	28	24	23			
%	54.3	62.7	57.5	48.3	48	47.9			

Table 4.—Comparison between the spider communities inhabiting the two faces of the same hedge (relative abundance of species is given in parentheses; * = 1 individual).

Foliage orientation	W-NW	E-SE
Number of species	38	32
Total individuals	257	210
Dominant species	<i>Mangora acalypha</i> (13.2%) <i>Zilla diodia</i> (13.2%) <i>Anyphaena accentuata</i> (6.5%)	<i>Philodromus cespitum</i> (24.8%) <i>Nigma puella</i> (6.6%) <i>Heliophanus</i> sp. (8%)
Not common	<i>Clubiona brevipes</i> (2.7%) <i>Theridion mystaceum</i> (1.5%) <i>Theridion pallens</i> (1.5%) <i>Atea triguttata</i> (1.5%) <i>Hyptiotes paradoxus</i> (1.2%) <i>Meta segmentata</i> (0.7%) <i>Leptyphantus tenuis</i> (0.7%) <i>Araneus umbraticus</i> (*) <i>Microlinyphia pusilla</i> (*) <i>Synaema globosum</i> (*)	<i>Theridion tinctum</i> (1.4%) <i>Anelosimus</i> sp. (1.9%) <i>Bathyphanes gracilis</i> (*)

There is no significant differences between the average number of species collected by linear meter in hedges B, C, D and E. The average density of individuals collected fell considerably for the two hedges of low value and for one of the hedge of high ecological value (B). The difference in the mean number of spiders collected between the two hedges A and B (high value) was strongly related to the presence of numerous immatures of four species or genera (*Zygiella* sp., *Nigma puella* (Simon 1870), *Araneus diadematus* Clerck 1758, *Dicyna uncinata* Thorell 1856) in hedge A. This was confirmed by the low value of the Shannon evenness index for that spider assemblage.

Influence of foliage orientation.—The orientation of the foliage may influence the structure of the spider communities since the percentage of shared species is higher between two hedges of the same foliage orientation (hedges B and F, west orientation) than be-

tween two of the same ecological value (Table 3). This hypothesis is supported by the comparison of the spider communities sampled on the two faces of the same hedge (Table 4). We observed a substitution among the three dominant species and 12 of the species collected on this hedge were not common to both faces of the hedge investigated. Moreover, the UGPMA analysis separated the six spider communities into three clusters which were not congruent with the respective ecological value of the hedges (Fig. 1). This can also be related to the foliage orientation since the cluster analysis separated group of hedges (A,D, or C) sampled on their eastern face. Thus, variation in the relative abundance of individuals observed among the six communities could not be correlated with the ecological value of the hedges.

Specific composition of spider communities.—The ANOVA shows that there is a significant difference between the relative abundance of each species in the three types of hedges (source A; P-value < 0.05), but the relative abundance of a same species collected in the three type of hedges is not significantly different (source B; P-value > 0.05). Furthermore, there is no significant interaction amongst the two factors which strongly suggests the lack of relationship between hedge type and the structure of the spider community associated (Table 5). This has to be connected with the fact that 90% of the individuals col-

Table 5.—ANOVA analysis of three community categories (low, medium, and high).

Source	df	MS	F-ratio	P-value
Main effects				
A: species	72	53.2	12.95	0.000
B: hedge type	2	<0.01	0.00	1.000
Interactions AB	146	2.44	0.6	0.1
Residual	222	4.11		

Table 6.—Dominant species in each hedge with relative abundance (in percentage).

	A	B	C	D	E	F
<i>Zygiella</i> sp.	23	4.5	18	17.5	9.7	13
<i>Nigma puella</i>	16.6	9.3	14	15.6		22.5
<i>Philodromus</i> sp.	5.7	5.7		9	9.9	5.9
<i>Zilla diodia</i>	5	12	6.3	9.6	7.5	5
<i>Dictyna uncinata</i>	6		6.5	6		8.5
<i>Araniella opisthographa</i>		9.8			11	9
<i>Anyphaena accentuata</i>			4.5			
<i>Araneus diadematus</i>	9.4					
<i>Heliophanus</i> sp.		15				
<i>Paidiscura pallens</i>					11	

lected belonged to shared species (Appendix 1). Among the 10 dominant species collected in each hedge (Table 6), 5 are the dominant species in all hedges. The dominance of *A. diadematus* and of *Heliophanus* sp. has to be related to the numerous immatures collected in only one of the hedges of high ecological value. The same remark can be made concerning the dominance of *A. accentuata* (hedge C) and *P. pallens* (hedge E). Therefore, if we consider the representation of adult spiders, there were no dominant species which were characteristic of hedges of low, medium, or high ecological value. In addition, the analysis of species distribution according to functional groups did not reveal a significant difference in the representativeness of the various groups (Table 7). Very few species (Table 8) were collected on only one of the six hedges, and each was represented by only 1 or 2 individuals. Some species were absent from hedges of high value (e.g., *Lathys humilis* Blackwall 1855, *Araneus triguttatus* (Fabricius 1775) or, on the contrary, species were always absent from hedges of low value (e.g.,

Gibbaranea gibbosa (Walckenaer 1802), *Saitis barbipes* Simon 1868).

DISCUSSION

Very few comparative studies have been made on the spider communities of the hedgerow networks, and they are mainly based on the analysis of ground living spiders (Petto 1990; Bergthaler 1996). This first approach to investigating foliage spider communities shows that there were no direct relationships between spider biodiversity and an index that described hedge habitat quality based on the analysis of the vegetation architecture. Therefore, concerning the spiders inhabiting the foliage, easy field indicator parameters of hedge quality, as for instance spider species composition or relative abundance of species, are not useful.

By artificially modifying the density of the foliage of a big sage (*Artemisia tridentata*), Hatley & MacMahon (1980) demonstrated that spider species diversity and the number of guilds were positively correlated with indicators of shrub volume and foliage diversity. These variations were observed on spider communities which were colonizing a shrubby layer composed by only one vegetal species. We also found that the hedge type may influence the composition of spider assemblage in the foliage. But, in the present case, because the architecture of the foliage is too diverse, whatever the ecological value of the hedge is, the spider specific richness remains almost the same for hedges of high or low ecological value. Moreover, it can be argued that foliage orientation, which was not incorporated into the index of vegetation quality, induced substitution of spider species, further limiting again

Table 7.—Number of species according to hunting habits for the different group of hedges.

	High value	Medi- an value	Low value	Total
Orb-web spiders	13	14	10	14
Frame-web spiders	11	11	13	16
Sheet-web spiders	9	6	9	16
Ambush hunters	11	8	9	12
Diurnal wanderers	12	10	10	16
Nocturnal wanderers	6	5	7	8

Table 8.—Single species in three categories of hedges (* Genus present in the two other types of hedges).

	Hedge quality		
	High	Medium	Low
Diurnal	<i>Salticus scenicus</i> <i>Pirata</i> sp.	<i>Bianor aurocinctus</i> <i>Pardosa hortensis</i>	<i>Alopecosa accentuata</i>
Nocturnal	<i>Micaria</i> sp.	<i>Agroeca</i> sp.	<i>Clubiona terrestris</i> *
Frame web	<i>Robertus arundineti</i> * <i>Robertus lividus</i> * <i>Philodromus dispar</i> *		<i>Theridion impressum</i> * <i>Theridion tinctum</i> * <i>Episinus</i> sp.
Ambush-hunters	<i>Ozyptila praticola</i> * <i>Tibellus</i> sp.		
Sheet-weavers	<i>Agyneta affinis</i> <i>Agyneta subtilis</i> <i>Pelecopsis parallela</i> <i>Walckenaeria acuminata</i>	<i>Agyneta rurestris</i> <i>Microlinyphia pusilla</i>	<i>Ceratinella brevipes</i> <i>Collinsia submissa</i> <i>Leptyphantes ericaeus</i> <i>Oedothorax fuscus</i> <i>Panamonops sulcifrons</i>

the ability of the index to reflect changes in spider diversity. This study also demonstrates that one hedge has to be carefully sampled on its two faces in order to identify the whole spider species inhabiting the foliage.

As density and specific diversity of spiders do not correspond to the general vegetal quality of hedges, are there any indicating species which show the habitat quality? The dominant species did not vary among hedges of different quality, which supports our former observations on the relatively stable composition of dominant species colonizing the shrubby layers within the same macroclimatic sector (Ysnel et al. 1996). However, the indicator species for the ecological quality of the hedges could be identified, not among the dominant species, but on the contrary, by considering the single species collected in one hedge. However, these species were poorly represented in the samplings and their absence from hedges of other quality could be sampling artifact or could be related to the foliage orientation of the hedge investigated. Some species are missing from the category of hedges with a high or low ecological value. These species, then, are likely to be more independent of the orientation of the hedges and their absence could be connected to the structure of the vegetation. Further investigations in other hedges of different ecological value are required to clarify these indicators. Concerning the maintenance of spider biodiversi-

ty, we must notice that the presence of hedge groups of different index on one area will lead to bigger specific diversity than the presence of only one edge group of high index.

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Appendix 1.—Total list of species with number of individuals collected in all the hedges.

Biological value of hedges	High		Medium		Low	
	A	B	C	D	E	F
Diurnal wanderers						
<i>Alopecosa accentuata</i> (Latreille 1817)					1	
<i>Anyphaena accentuata</i> (Walckenaer 1802)	33	11	35	20	5	5
<i>Ballus biimpressus</i> (Doleschall 1852)	14	13	4	7	7	1
<i>Bianor aurocinctus</i> (Ohlert 1865)				2		
<i>Ero aphana</i> (Walckenaer 1802)	6		8	5	1	1
<i>Evarcha</i> sp.		1			2	
<i>Heliophanus cupreus</i> (Walckenaer 1802)		13				1
<i>Heliophanus</i> sp.	19	61	2	15	4	13
<i>Macaroeris nidicolens</i> (Walckenaer 1802)	3	1	13	8	3	1
<i>Pardosa hortensis</i> (Thorell 1872)				1		
<i>Pardosa</i> sp.	1				1	
<i>Pirata</i> sp.	2					
<i>Pisaura mirabilis</i> (Clerck 1758)			1	1	1	
<i>Saitis barbipes</i> Simon 1868	2	1		3		
<i>Salticus scenicus</i> (Clerck 1758)		1				
<i>Zora</i> sp.	1			1		
Nocturnal wanderers						
<i>Agroeca</i> sp.				1		
<i>Cheiracanthium</i> sp.	3	1		3		1
<i>Clubiona brevipes</i> (Blackwall 1841)		6				5
<i>Clubiona compta</i> Koch C.L. 1839		5		1	13	
<i>Clubiona terrestris</i> Westring 1851					1	
<i>Clubiona</i> sp.	28	19	39	21	26	7
<i>Micaria</i> sp.	1					
<i>Zelotes</i> sp.	1	5	1			2
Frame-web spiders						
<i>Anelosimus vittatus</i> (Koch C.L. 1836)	14	3	17	7	20	4
<i>Dictyna uncinata</i> Thorell 1856	63	12	51	38	6	30
<i>Episinus</i> sp.					1	
<i>Lathys humilis</i> Blackwall 1855			25	1	6	
<i>Nigma puella</i> (Simon 1870)	172	39	108	98	5	80
<i>Paidiscura pallens</i> (Blackwall 1834)	9	5	12	21	52	12

Appendix 1.—Continued.

Biological value of hedges	High		Medium		Low	
	A	B	C	D	E	F
<i>Robertus arundineti</i> (Cambridge O.P. 1871)	2					
<i>Robertus lividus</i> (Blackwall 1836)	1					
<i>Robertus</i> sp.				3	1	
<i>Theridion impressum</i> Koch C.L. 1881					1	
<i>Theridion mystaceum</i> Koch L. 1870	25	1	11	6	9	14
<i>Theridion tinctum</i> (Walckenaer 1802)						2
<i>Theridion varians</i> Hahn 1831	7	2	21	1	7	3
<i>Theridion</i> sp.	50	20	102	16	51	26
Orb-weavers						
<i>Araneus diadematus</i> Clerck 1758	98	18	2	12	2	1
<i>Araneus sturmi</i> (Hahn 1831)	1	2	1	1	5	
<i>Araneus triguttatus</i> (Fabricius 1775)			1	4	3	
<i>Araniella opisthographa</i> (Kulczynski 1905)	28	41	30	22	56	32
<i>Argiope bruennichi</i> (Scopoli 1772)	3	2		1		
<i>Cyclosa conica</i> (Pallas 1772)	1			1		
<i>Gibbaranea bituberculata</i> (Walckenaer 1802)		3	7	24	5	1
<i>Gibbaranea gibbosa</i> (Walckenaer 1802)	1	1	2	4		
<i>Larinioides cornutus</i> (Clerck 1758)	2		5		1	
<i>Mangora acalypha</i> (Walckenaer 1802)	18	12	17	20	11	4
<i>Tetragnatha montana</i> Simon 1874		2		1		
<i>Tetragnatha</i> sp.	17	11	16	11	21	7
<i>Zilla diodia</i> (Walckenaer 1802)	52	50	49	60	37	17
<i>Zygiella</i> sp.	240	19	140	110	48	46
Sheet-weavers						
<i>Agyneta affinis</i> (Kulczynski 1898)		1				
<i>Agyneta rurestris</i> (Koch C.L. 1836)				2		
<i>Agyneta subtilis</i> (Cambridge O.P. 1863)	3					
<i>Bathypantes gracilis</i> (Blackwall 1841)	1			1		
<i>Ceratinella brevipes</i> (Westring 1851)					2	
<i>Collinsia submissa</i> (Koch L. 1879)						1
<i>Hypomma cornutum</i> (Blackwall 1833)	2				5	
<i>Lepthyphantes ericaeus</i> (Blackwall 1853)					1	
<i>Lepthyphantes tenuis</i> (Blackwall 1852)	8		1	2	1	
<i>Lepthyphantes</i> sp.	14	1	8	4	3	2
<i>Microlyniphia pusilla</i> (Sundevall 1830)				1		
<i>Oedothorax fuscus</i> (Blackwall 1834)					1	1
<i>Panamonops sulcifrons</i> (Wider 1834)					1	
<i>Pelecopsis parallela</i> (Wider 1834)	1	1				
<i>Porrhomma oblitum</i> (Cambridge O.P. 1870)	1		1		1	1
<i>Walckenaeria acuminata</i> (Blackwall 1833)	1					
Ambush-hunters						
<i>Diaea dorsata</i> (Fabricius 1777)			1		1	
<i>Misumenops tricuspidatus</i> (Fabricius 1775)	8	1	5	2	2	4
<i>Ozyptila praticola</i> (Koch C.L. 1837)	3					
<i>Ozyptila</i> sp.	1	1	12		4	1
<i>Philodromus cespitum</i> (Walckenaer 1802)	3	5	2	2		5
<i>Philodromus dispar</i> (Walckenaer 1802)	1					
<i>Philodromus rufus</i> (Walckenaer 1802)	1	1	1	2	6	
<i>Philodromus</i> sp.	60	24	29	57	49	21
<i>Synaema globosum</i> (Fabricius 1775)		1	4		1	
<i>Tibellus</i> sp.	1					
<i>Tmarus stellio</i> Simon 1875	2				1	
<i>Xysticus</i> sp.	6			3	1	2

EFFECT OF RIVER FLOW MANIPULATION ON WOLF SPIDER ASSEMBLAGES AT THREE DESERT RIPARIAN SITES

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ABSTRACT. The distribution, abundance, and diversity of wolf spider (Lycosidae) assemblages were investigated via pitfall trapping at three sites near Granite Reef Dam outside Phoenix, Arizona. These three sites featured different moisture and temperature regimes due to the dam, which diverts the Salt River into an urban canal system. Site 1 was a natural riparian area above the dam along the Salt River, Site 2 was adjacent to a man-made diversion canal, and Site 3 was adjacent to the dry riverbed below the dam. Four lycosid species were found at Site 1, with *Pardosa vadosa* Barnes 1959 dominating. Two species each, though very few total individuals, were found at Sites 2 and 3. Simpson's index of diversity (of lycosids and of all other terrestrial arthropods) was higher for Site 1 than for Sites 2–3. Prey availability was comparable among sites, but Site 1 had significantly higher relative soil moisture levels and less extreme substrate and air temperature conditions than did Sites 2 and 3. Spider abundance at each site was independent of prey availability, but instead depended chiefly upon moisture and temperature regimes among sites. The results suggest that wolf spiders experienced a significant effect from disturbance of their habitat by the dam, and that abiotic habitat attributes such as moisture and temperature may be more important for wolf spider abundance than prey availability alone in desert riparian systems.

Keywords: *Pardosa*, Salt River, Arizona

In comparison to habitats featuring less human impact, urbanization can have significant effects on the environmental conditions, populations, and community structures of ecological systems (McDonnell et al. 1997). While vertebrate populations often may decline due to the anthropogenic pressures and habitat loss associated with urbanization (for example: Hoi Leitner 1989; Gill & Williams 1996), many invertebrate species exhibit an ability to establish alternative ecological relationships allowing them to persist or even flourish in urban environments (Frankie & Ehler 1978; Dreistadt et al. 1990). As a result, arthropod populations and assemblages may be similar among natural and disturbed sites (Frankie & Ehler 1978). As one might expect, however, urbanization has also been shown to have adverse effects on some invertebrate populations (Nowakowski 1986; Sawoniewicz 1986; Ruszczyk & Mellender 1992). Frankie & Eh-

ler (1978) point out that perhaps one of the few generalizations which can be made about terrestrial invertebrate populations in urban environments is that the distribution and diversity of such species often reflect different moisture regimes.

As part of the newly-funded Urban Long Term Ecological Research site in central Arizona, we set out to compare the distribution and diversity of assemblages of wolf spiders (Lycosidae) in three Sonoran Desert riparian areas featuring different environmental regimes as a function of river flow manipulation. We sought to investigate the relationships between wolf spider distribution and abundance patterns to prey availability, temperature regimes (air temperature, substrate temperature, and variation between the two), and relative soil moisture.

Most wolf spiders do not build webs, but rather are vagrant hunters, and spend most of their time near the ground surface. They may wander or remain stationary while hunting until a prey item is detected by visual or vibratory cues, at which point they attack (Kaston

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1978; Kronk & Riechart 1979; Cady 1984; Persons & Uetz 1996). Different species of *Pardosa*, the dominant genus found in this study, have been variously described as either sit-and-wait or cursorial hunters (Morse 1997). A large body of research has demonstrated that wolf spiders exhibit habitat selection and distribution and abundance patterns based on a variety of factors, including: prey availability, capture efficiency, mating probability (in males), herbaceous vegetation cover, temperature, humidity, and soil moisture content (e.g., Cherrett 1964; Hallander 1967, 1970; Lowrie 1973; Kronk & Riechart 1979; Bultman 1992; Cady 1984; Moring & Stewart 1994). Microenvironmental factors such as vegetation cover, temperature, humidity, and prey availability can be directly related to substrate moisture levels.

Based on these studies, we expected that mid-summer censuses (when the abiotic conditions of the desert were at their most extreme) would result in wolf spider assemblages that varied as a function of habitat. In particular, we expected wolf spider abundance and species diversity to depend sensitively on soil moisture as in Kronk & Reichert's (1979) study of *Rabidosa santrita* (Chamberlin & Ivie 1935) and as in Agnew & Smith's (1989) study of spiders in irrigated and drought-stressed peanut fields. Experiments demonstrating the inability of *Pirata piraticus* (Clerck 1757) to tolerate desiccation (Cherrett 1964), as well as the association of many western *Pardosa* species with moist habitats (Lowrie 1973) further supported our expectations.

STUDY SITES AND METHODS

The study sites were two desert riparian areas adjacent to the Salt River and one area along a canal, running through Tonto National Forest near Granite Reef Dam, 22 km east of downtown Phoenix, Arizona. Completed in 1908, Granite Reef Dam is the point where the Salt River is diverted into man-made canals for eventual human use (Higgs 1995). The presence of this water resource is one of the key factors that has facilitated explosive growth of the Phoenix metropolitan area in the last several decades. Because of the river diversion, the riverbed below the dam is nearly completely dry for much of the year. Prior to the completion of Granite Reef Dam, downstream reaches were well-watered and fea-

tured desert riparian vegetation typical of upstream areas today (see below). However, Granite Reef Dam is only the most recent modification to the river and surrounding riparian corridor: this portion of the river was also the site of large-scale water diversions into irrigation canals by the Hohokam culture (AD 700–1450) (Gregory 1991).

Site 1 was a strip of riparian area approximately 7 km upstream of the dam in a semi-natural area designated for recreational use. Immature willow (*Salix gooddingii* and *Salix exigua*), cottonwood (*Populus fremontii*), and tamarisk (*Tamarix* spp.; invasive exotics) trees as well as understory riparian vegetation grew along the river bank; the substrate was primarily rock cobble and sand. Site 2 was about 2 km downstream of the dam adjacent to one of the diversion canals. Because the canals were constructed of concrete, which allows for little lateral movement of water outward from the sides of the canal, plant cover at this site, even that immediately adjacent to the canal, was typical upper Sonoran Desert vegetation featuring saguaro cactus (*Carnegiea gigantea*) and palo verde (*Cercidium microphyllum*). The substrate was primarily densely packed sand. Site 3 was an area about 0.5 km downstream of the dam running along the dry riverbed where the river formerly flowed. It featured a mixture of upper Sonoran vegetation and riparian species able to persist on the water and disturbance regime provided by low-volume, irregular releases of water from the dam; the substrate was primarily a mixture of sand and cobbles.

At two locations in each of the three sites, we placed a set of ten pitfall traps (spaced 2 m apart in two rows of five) with the first row located about 2 m away from the adjacent water source (or edge of dry riverbed) and running parallel to it. Traps (plastic drinking cups ["Dixie[®]"] 9 cm in diameter) were buried in the ground with the rim set flush with the surface. A second cup, with the top 3 cm cut off, was placed in each buried cup for periodic removal of specimens. Forest service regulations, concerns over public access (especially pets), and the intense heat and evaporative potential of the Sonoran Desert region during the summer, mandated that we use "dry" pitfall traps (e.g., Hurd & Fagan 1992) rather than traps containing chemical preservatives. To provide a vertical dimension to the trap (and

thus refugia for captured animals), we placed a loosely crumpled piece of toweling paper in the bottom of each trap. Trapped spiders and other arthropods were collected every 3–6 days. Spiders were sorted to species (using Kaston 1978 and Roth 1993), and broken down into age (sub-adult, adult) and sex categories. Species identifications based on representative specimens were established by Dr. David Richman (New Mexico State University). Voucher specimens have been deposited in the Central Arizona Phoenix LTER's arthropod collection, which is associated with other natural history collections at Arizona State University (ASU). Other arthropods were sorted to family or order, as possible. We also used dry cup pitfall trapping to provide an estimate of available prey, which included counting all soft-bodied arthropods that did not exceed the average length of the largest wolf spider species found (as in Moring & Stewart 1994). This means that we counted only small, immature, and soft-bodied individuals of Formicidae, Dermaptera, and Coleoptera. Our estimate of available prey thus may be an underestimate for large bodied wolf spiders that have sometimes been observed feeding on hard-bodied insects (e.g., Coleoptera, Orthoptera [Nyffeler & Benz 1988]). Although the inability of lycosids to climb up the smooth surfaces of pitfall traps does not preclude the use of dry pitfall trap data for wolf spiders, many potential insect prey may walk or fly out of such traps or be preyed upon by lycosids while in the traps, which means that our arthropod data are likely underestimates.

Traps were in place from 11 June 1998–13 July 1998, although a rising river level behind the dam (due to early arrival of the monsoon season in the Sonoran Desert) washed out all traps at Site 1, forcing the early termination of arthropod collection on 30 June 1998 at that site. After finding (1) no discernable differences between trapped arthropods at Sites 2 and 3 between the periods 11 June–30 June 1998 and 30 June–13 July 1998 and (2) no temporal trends in abundance at Site 1, we corrected for the different numbers of trap days by multiplying all counts at Site 1 by 32/17. Our results are comparable if we restrict our analyses to data taken from all three sites between 11 June–30 June 1998. Temperature readings were taken at selected locations near

each set of traps at each site over four non-consecutive, sunny days, with four readings being taken at each plot every hour between the hours of 0700–1100 h. Both ground temperatures and air temperatures (with the thermometer held 2 cm above the ground) were taken. Soil moisture readings were taken with a soil moisture probe (measuring relative percent soil moisture) on one day with five measurements being taken at Sites 2 and 3. Six readings were taken at Site 1 (three at each sub-site) as more variable soil moisture levels were found.

RESULTS

Pardosa vadosa Barnes 1959 was by far the most common lycosid in the vicinity of Granite Reef Dam, comprising well over 90% of the individual lycosids captured (Table 1). *Pardosa vadosa* (5–6 mm as adults) was also the only lycosid found at all three sites. For this species, 54% of the mature, identifiable individuals were female, indicating a relatively balanced sex ratio during the sampling period. In addition, *P. vadosa* was the only species for which a large number of sub-adults was collected. This is potentially important because it could indicate that other lycosids may reproduce at different times of the year than *P. vadosa*, which could lead to markedly different abundance patterns through time. *Arctosa littoralis* (Hentz 1844) (adult size 12–15 mm), which was found only at Site 1, was the next most common lycosid as determined by pitfall trap collections. *Sosippus californicus* Simon 1898 (adult size 12–16 mm) was also found only at Site 1, but in low numbers. *Allocosa subparva* Dondale & Redner 1983 (adult size 4–5 mm) was found at both Sites 1 and 3, but in low numbers at the latter site, while *Pardosa* sp. #2 was found only at Site 2, again in low numbers. After lycosids, the Gnaphosidae was the next most common family of spiders caught in the pitfall traps.

Pitfall trapping indicated wolf spiders were more abundant at Site 1 than at Sites 2–3 (Table 1). This pattern held for male, female, sub-adult, and unidentifiable individuals (sex unidentifiable due to severe desiccation and/or cannibalism in traps). Roughly 16% of collected wolf spiders appeared to have been attacked by other spiders while inside the dry pitfall traps.

Other arthropods commonly represented at

Table 1.—Total counts of each arthropod group at each site, with lycosids separated into species. All Site 1 traps were destroyed on day 18. Site 1 specimen counts are corrected for differential trap-days by multiplying by 32/17.

	Site 1-A*	Site 1-B*	Site 1 (pooled*)	Site 2-A	Site 2-B	Site 2 (pooled)	Site 3-A	Site 3-B	Site 3 (pooled)
Lycosidae									
<i>Pardosa vadosa</i> (total)	602	652	1254	3	0	3	0	2	2
Female	171	168	339	2	0	2	0	1	1
Male	139	149	288	0	0	0	0	0	0
Sub-adult	136	288	424	1	0	1	0	1	1
Sex unidentifiable	156	47	203	0	0	0	0	0	0
<i>Pardosa</i> sp. 2 (total)	0	0	0	3	0	3	0	0	0
Female	0	0	0	0	0	0	0	0	0
Male	0	0	0	0	0	0	0	0	0
Sub-adult	0	0	0	3	0	3	0	0	0
<i>Arctosa littoralis</i> (total)	32	10	42	0	0	0	0	0	0
Female	11	6	17	0	0	0	0	0	0
Male	19	4	23	0	0	0	0	0	0
Sub-adult	0	0	0	0	0	0	0	0	0
Sex unidentifiable	2	0	2	0	0	0	0	0	0
<i>Allocosa subparva</i> (total)	14	0	14	0	0	0	0	1	1
Female	6	0	6	0	0	0	0	1	1
Male	6	0	6	0	0	0	0	0	0
Sub-adult	0	0	0	0	0	0	0	0	0
Sex unidentifiable	2	0	2	0	0	0	0	0	0
<i>Sosippus californicus</i> (total)	6	2	8	0	0	0	0	0	0
Female	2	2	4	0	0	0	0	0	0
Male	4	0	4	0	0	0	0	0	0
Sub-adult	0	0	0	0	0	0	0	0	0
Gnaphosidae	9	21	30	16	2	18	0	2	2
Salticidae	0	0	0	1	0	1	1	4	5
Clubionidae	0	2	2	1	1	2	0	0	0
Oxyopidae	0	0	0	1	0	1	0	0	0
Theridiidae	0	0	0	0	0	0	1	3	4
Unknown spiders	2	0	2	11	10	21	4	8	12
Formicidae	1020	446	1466	521	782	1303	1298	1193	2491
Coleoptera	200	597	797	126	163	289	107	171	278
Isopoda	1316	85	1401	39	7	46	30	35	65
Acarina	2	184	186	74	55	129	132	60	192
Collembola	0	0	0	78	100	178	11	25	36
Dermaptera	171	32	203	0	0	0	0	0	0
Scorpiones	0	21	21	5	25	30	9	7	16
Miscellaneous available prey	2	17	19	43	26	69	9	31	40
Total available prey	1067	632	1699	625	708	1333	1258	1121	2379

these sites included members of the taxa: Formicidae, Isopoda, Coleoptera, Acarina, Collembola, Dermaptera, and Scorpiones. Formicids comprised the dominant group at all sites. Kendall's rank correlation analyses of the relative abundance of the top ten arthropod groups found at each subsite indicated greater

intrasite variability at Site 1 than at Sites 2–3 (Table 2). In addition rank correlation analyses indicated substantial differences in relative abundance of different arthropod groups between Site 1 and Sites 2–3. However, Sites 2–3 harbored strikingly similar arthropod assemblages overall (Table 2).

Table 2.—Rank correlation coefficients for arthropod assemblages within and among pitfall sampling sites. Analyses involve the 10 most common arthropod groups except for analyses involving Site 3 in which only 9 groups were sufficiently common for analysis. * = significant at $P = 0.05$, ** = significant at $P = 0.01$.

Sites compared	Rank correlation coefficient
Sub-sites at Site 1:	0.547*
Sub-sites at Site 2:	0.786**
Sub-sites at Site 3:	0.983**
Site 1 vs. Site 2:	0.442
Site 1 vs. Site 3:	0.569
Site 2 vs. Site 3:	0.940**

Dominance-diversity curves (Fig. 1) also reveal striking differences among sites. Arthropod collections at Site 1 are dominated by four groups of arthropods (Formicidae, Iso-poda, *Pardosa vadosa*, and Coleoptera), whereas Formicidae are clearly dominant at Sites 2 and 3. Calculating Simpson's index of diversity also indicates higher terrestrial arthropod diversity at Site 1 (0.781) compared with Sites 2 and 3 (0.553 and 0.349, respectively). Wolf spider abundance at each site showed no correlation with available prey (Kendall's rank correlation; Fig. 2). Total wolf spiders collected at Site 1 far exceeded those collected at Sites 2 and 3, but available prey varied only slightly between sites.

Average morning air and substrate temperatures at Site 1 were lower than comparable averages from Sites 2 and 3 (MANOVA, Wilks' Lambda = 0.572, $P < 0.001$). In addition, substrate temperatures at Sites 2 and 3 were on average 2.4 °C and 1.5 °C higher, respectively, than corresponding air temperatures, while at Site 1 (the natural river site) average air and substrate temperatures were virtually identical. At Site 1, substrate temperatures on the cobblestones were generally warmer than the air and the soil was generally cooler. The relative abundance of lycosids decreased as air temperature, substrate temperature, and the temperature difference between air and substrate increased (Fig. 3). Relative abundance of wolf spiders also increased with increasing relative soil moisture among sites. At Site 1, where relative soil moisture ranged from 50–70%, wolf spiders represented between 20–35% of the pittrapped fauna.

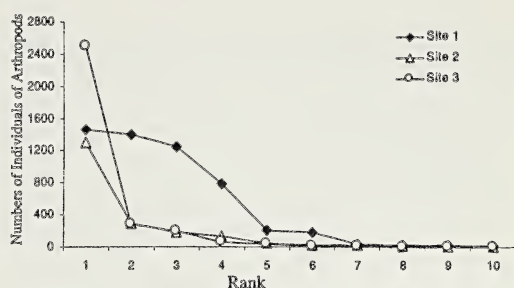


Figure 1.—Dominance diversity curves of the 10 most abundant groups of arthropods at each site. Counts from Site 1 are sums of actual and projected counts.

In contrast, at Sites 2 and 3, where relative soil moisture ranged from 0–10%, wolf spiders represented less than 2% of the pittrapped specimens.

DISCUSSION

Overall, abiotic conditions and the diversity of available prey appear to influence wolf spider diversity and abundance in riparian and pseudo-riparian areas near Granite Reef Dam in central Arizona. In particular, the less extreme moisture and temperature regimes of the riparian habitat at Site 1 likely facilitated the greater abundance of wolf spiders there. Although substrate temperature was consistently higher than air temperature at Sites 2 and 3, substrate temperature differed little from air temperature at Site 1, where high soil moisture levels likely contributed to a cooling effect. Experimental studies of microhabitat

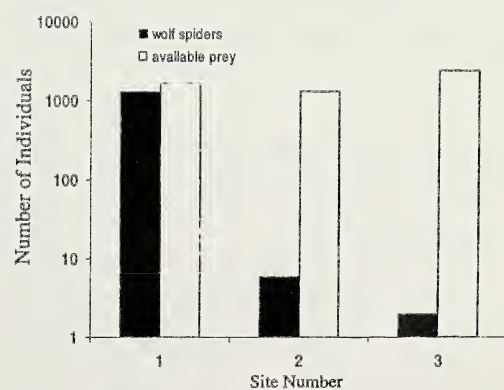


Figure 2.—Total lycosids trapped at each site compared to total available prey. Available prey included all soft-bodied arthropods that did not exceed the average length of the largest wolf spider species found. Note logarithmic y-axis.

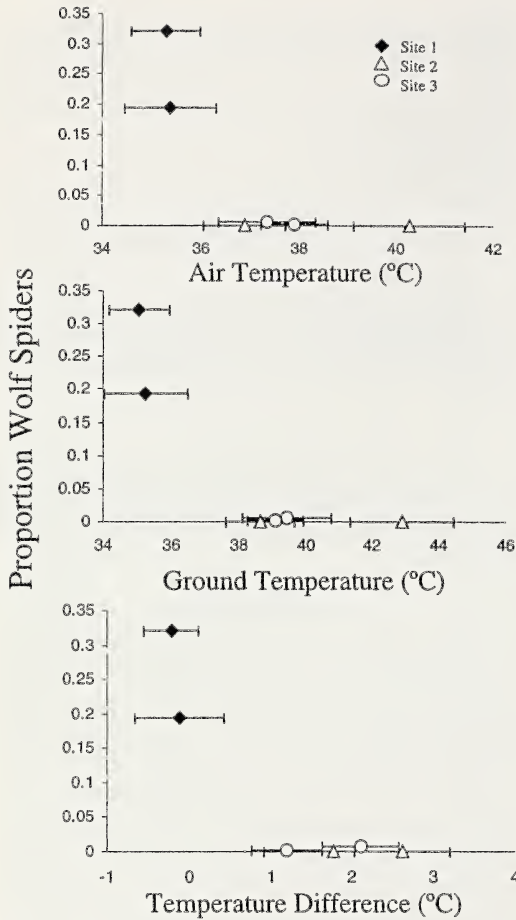


Figure 3.—The proportion of wolf spiders (all species) at each sub-site as a function of temperature regimes. Temperature readings were taken in early to mid-morning, before the most thermally-oppressive part of the day. Air temperature was taken approximately 2 cm above the ground surface. Error bars give standard errors of temperature readings.

selection at Site 1 could support or refute the idea that spiders are actually selecting the riverside for (at least in part) its less extreme temperatures.

Wolf spider abundance and diversity were also positively related to relative soil moisture among sites. These results agree strongly with our prediction that we would find the greatest abundance and diversity of wolf spiders by the natural river upstream of the dam, due to the importance of proximity to water and moist soil for lycosid distributions (Cherrett 1964; Kronk & Riechert 1979; Cady 1984; Agnew & Smith 1989; Bultman 1992). Indeed, Low-

rie (1973) has shown that moisture is a key factor in the fairly specific habitat preferences of many species of *Pardosa*, the dominant genus found in this study.

In general, prey availability has been shown to be an important aspect of spider habitat association (Kronk & Riechert 1979; Moring & Stewart 1994; Henshel & Lubin 1997). But, because wolf spiders are known to require a variety of food items in order to reach maturity (Uetz et al. 1992), higher species diversity at Site 1 as opposed to the overall abundance of prey species (Fig. 2) may contribute to increased wolf spider abundance there. Similar plant species composition at Sites 2 and 3 likely contributes to the strong rank correlation among groups of arthropods between those sites, especially with respect to herbivorous insects (Table 2).

All analyses of prey availability, however, must be viewed in the light that pitfall trapping is a sampling method with differential capture success among species. For instance, pitfall traps sample not the true density, but rather the "active density" of wandering arthropods in an area over a given time (Uetz & Unzicker 1976; Uetz 1977). The dry pitfall traps likely under-sampled potential insect prey, as mentioned above, especially Diptera, which may comprise a significant component of *Pardosa* diet (Hallander 1970; Morse 1997; Nyffeler & Benz 1988; Nyffeler & Breene 1990). Predation by the numerous spiders in the dry traps at Site 1 may also have reduced prey availability at that site, possibly accounting for the similarity in prey abundance collected at each site. Pitfall traps are still useful, however, in estimating the number of species of wandering spiders present over a wide range of habitats (Uetz & Unzicker 1976).

Although we lack data on spider distributions prior to dam construction, the results of this study suggest that wolf spider assemblages may have been substantially affected by dam construction, water diversion, and subsequent changes of the riparian vegetation in the vicinity of Granite Reef Dam. Our results support the hypotheses that desert riparian wolf spider-habitat associations are strongly influenced by soil moisture and substrate-air temperature regimes and that abundance of available prey alone may not be a good predictor of wolf spider distributions.

The impacts of urbanization on spider as-

semblages are worth investigating because spiders are not only an important food source for birds, lizards, wasps, and other species; but, when viewed as an assemblage of generalist predators, they may also play an important role in the regulation of insect populations (Riechert & Lockley 1984; Settle et al. 1996; Morse 1997; Skerl 1997). Overall, the study of the ecological consequences of urbanization for particular groups of plants and animals is important because it can indicate the degree of disturbance of their environments and may be useful in developing strategies for conservation (Ruszczyk & Mellen-der 1992). Although this research was specifically designed as a summer study, when the desert environment was at its most extreme, it would be interesting to investigate if the striking patterns observed here persist within and among years, when the desert riparian sites experience a greater range of environmental conditions.

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RESEARCH NOTE

EXTENDED NEST RESIDENCE AND CANNIBALISM IN A JUMPING SPIDER (ARANEAE, SALTICIDAE)

Keywords: Sociality, parental care, matrophagy, sub-social

Menemerus bracteatus (L. Koch 1879) is a large unidentate Australian salticid that nests under the bark of eucalypt trees (Davies & Żabka 1989). During an earlier work (Rienks 1992) several nests were found on the scribbly gum, *Eucalyptus racemosa* Cavanilles. While studying the microhabitats of a wide range of salticid species, it was noted that sometimes a single nest of this species was occupied by numbers of large juveniles and the dead and shrunk body of a conspecific adult female, possibly the mother. It is common for juvenile salticids to remain with the mother for the first instar after emerging from the postembryo stage (Richman & Jackson 1992), but nest sharing by larger juveniles and an adult female is unusual. My observations suggested the juveniles of *M. bracteatus* may feed on their mother, a behavior known as matrophagy. Matrophagy, although known in a variety of spider families, has not been documented for salticids. In the present paper, I provide data on nest structure, nest residence and predators other than conspecifics. Also, I examine the hypothesis that juveniles of *M. bracteatus* cannibalize their siblings and practice matrophagy. Voucher specimens have been lodged with the Queensland Museum (QM S.47193).

Four study sites in forests in which the scribbly gum was common were selected in the Brisbane metropolitan area. Three sites were in Toohey Forest, Griffith University Campus; and one was in woodland adjacent to Tingalpa Reserve. In each site, I sampled the occupants of as many nests as possible. No nests were found in the first search which was made when the scribbly gums had just begun shedding bark (late October to early November). A search between late December and early January revealed 35 nests in various stages of construction, 24 of which contained

at least one clutch. A further seven nests found were from the previous season (evidence: constructed on older bark attached to the shedding bark, and contained shed exoskeletons only).

Description of nests.—Nests were constructed in the curve of the shedding bark and had tough roof and outer walls which strongly adhered to both the shedding bark and the tree trunk. Each nest had two reinforced entrances with projecting lip-like flaps above and below the entrance slit which may hinder access by predators and parasites. Nests were very strongly constructed and could be removed intact by carefully pulling the loose bark piece away from the tree trunk.

Most nests appeared to be in an early stage of construction. Of the 11 nests which contained no clutches, seven appeared to have been just begun and consisted of the outer walls only (three of these contained adult females), while the other four contained what appeared to be preyed-upon clutches (stained mass in which some individual chorions could be distinguished) and may have been abandoned. Counts were made of the number of clutches, and the number of eggs per clutch in each nest for 23 nests. A total of 54 clutches (median of two per nest) were found: 26% of the 23 nests contained one clutch, 30% contained two, 30% contained three and 13% contained four or more. Nests containing four or more clutches were completely filled with clutches and densely packed with loose sheets of very sticky silk laid down between successive clutches. In contrast, nests with fewer clutches were only partially filled with a conspicuous gap between the nest contents and the nest roof.

The number of eggs per clutch was between 9–45 (mean 23.8, SD 6.9, $n = 32$) Eggs were

Table 1.—Stages found in previous season's nests of *Menemerus bracteatus*. Numbers marked with an asterisk are nests in which adult remains were found. Nest 1, which may have been from the 1995–6 season, had been subjected to substantial insect attack; and its contents were almost entirely gone, leaving the outer nest wall only. Remains of individuals that had apparently been preyed upon are indicated by the number found, followed by "p". Instar determination is based on size of the carapace of the shed exuviae.

Nest	Larva	First instar	Second instar	Third instar	Fourth instar	Fifth instar	Sixth instar
1	0	0	0	0	0	1	0
2*	19	25	32 + 1p	11 + 1p	0	0	0
3	27	26	35	22	0	0	1
4	27	25 + 2p	18	7	0	0	0
5*	35	19	24	18	4	1	0
6	36	36	26	29	2	0	0
7	26 + 1p	27 + 1p	26 + 1p	13	10	0	2

pale orange in color, did not adhere to each other, and were enclosed in a loose bag of non-sticky silk. Regardless of whether they were developing or apparently preyed-upon, clutches were included in calculations if the original numbers of eggs could be accurately determined. Numbers of eggs per clutch (clutch size) did not vary significantly with apparent order of laying (outermost clutch taken to be the most recent). Of the 23 nests in which clutches were examined in detail, the oldest stage of development included the egg (57% of nests), embryo (9%), prelarva (4%), larva (13%), first instar (13%) and second instar (4%) (terminology after Foelix (1996) which follows that of Vachon (1957)).

In total, 43% of the nests had one or more clutches showing signs of development. Three nests contained a clutch consisting of eggs, developing eggs, and prelarvae and/or larvae, suggesting that development of eggs within a clutch tends not to be synchronous. In two nests containing four or more clutches, clutch development showed a cohort effect with separation of cohorts by up to one instar (i.e., modal numbers at every second stage). One of these nests contained 2–3 clutches of eggs (total of 71 eggs), 31 larvae and 34 first instars. The second nest contained one clutch of eggs (25 eggs), 19 prelarvae, 7 larvae, 31 first instars and 5 second instars.

Nest residence by juveniles.—The seven nests collected that were from the previous (1996–7) season contained shed carapaces and exoskeletons of, in total, seven distinct stages, including the larval stage and six instars (Table 1). The largest carapace was considerably

smaller than adult-sized. The numbers of carapaces at each stage was more or less constant from the larval stage through to the third and sometimes the fourth instar (as shown by second and third instar carapaces). Numbers then declined rapidly, suggesting that dispersal had occurred in the third and fourth instars. If nests of this species usually contain about four clutches then it appears that the number of juveniles that survived to disperse as fourth (or occasionally third or fifth) instars, was equivalent to 1–1.5 full clutches. The presence of carapaces of large juveniles (fifth instar and older) suggested that juveniles may use the natal nest as a retreat for five or more instars.

Cannibalism in the nest.—Sometimes entire clutches, still enclosed in the silk bag, contained empty chorions, and had apparently been eaten. Such clutches were found in the nests from both seasons. Also, I found several apparently preyed-upon individuals (larvae and later stages) in three nests from the previous season (Table 1). Two of the current season's nests that contained four clutches and were more developed than the other nests were examined in more detail for signs of cannibalism. All first and later instars in both of these nests had grossly enlarged abdomens, consistent with having recently fed. All larvae had small abdomens which were similar in size to those of the prelarvae, suggesting that they had not fed.

It appears that more clutches are laid than survive to disperse (see above). Since the number of larval carapaces in the previous season's nests never exceeded 36 (the equivalent of just over one clutch), it is likely that

the older instars preyed upon prelarvae and larvae in addition to eggs.

Two nests from the previous season contained what were apparently adult remains, in one case the dorsal part of the carapace of an adult-sized individual, and in the other case, trachea attached to fragments of abdominal cuticle. It was not possible to determine whether these remains were those of adult females.

Predation.—Of the 23 nests collected in the 1997–8 season that were examined in detail, 26% contained one or two larvae of *Austromantispa imbecilla* (Gerstaecker) (Neuroptera: Mantispidae). The mantispid larvae from each of these nests, all of which initially contained either two or three clutches, were reared until pupation. In all cases, only a few eggs and larvae survived, the rest apparently being consumed by the mantispid. Four other nests contained clutches that had apparently been preyed upon by other predators. In total, 43% of 23 nests contained preyed-upon clutches with some nests having one (22% of nests), two (17%) or three (4%) clutches affected.

The young of *M. bracteatus* postpone dispersal from the natal nest until between the third and fifth instars, far later than is observed for most salticids. Another example of extended nest residence may also occur in *Hypaeus cucullatus* Simon 1900, because females and groups of juveniles of various sizes have been observed to share nests in this Central American salticid (Jackson 1989), but examples of juveniles cohabiting beyond the first and second instar are better known in maternal-social web-building spiders (Tretzel 1961, in Shear 1970; Kullmann 1972), and in spiders with more extended sociality (Jacson & Joseph 1973; Seibt & Wickler 1987; Evans et al. 1995).

In *M. bracteatus*, the extended nest residence, and the consequent large size attained by juveniles before dispersing, may be facilitated by the laying of multiple clutches in the same nest. This provides opportunity for juveniles to feed upon sibling eggs and probably also larvae and prelarvae. The finding of adult remains in old nests suggests that, as in many maternal-social (Bristowe 1958; Tretzel 1961, in Shear 1970; Kullmann 1972) and permanent social species from families other than the Salticidae (Jacson & Joseph 1973; Seibt

& Wickler 1987; Evans et al. 1995), matrophagy may occur in this salticid species. Perhaps the adaptive significance of the long duration of nest residence by juveniles may be primarily facilitation of matrophagy.

The laying of multiple clutches in the same nest probably does, however, have drawbacks. For other salticids comparable to *M. bracteatus* in size (females ranged from 9.5–11.5mm), the interval between oviposition of successive clutches tends to be 20–30 days. Assuming that the inter-clutch interval is comparable for *M. bracteatus* it is probable that a maternal female would need to make intermittent feeding forays away from the nest during the time span required for multiple oviposition. While at the nest, the female may be able to guard her eggs against the attacks of predators and parasites, but leaving the nest to feed would be likely to expose her broods to higher risks of attack by other spiders, ants, beetles and acrocerid flies and so forth (Austin 1985). The tough nest construction and complex, dense sticky silk packing of *M. bracteatus* nests may provide an exceptionally difficult barrier for enemies to penetrate when the maternal females is away (see Austin 1985), but the protection provided appears to be limited. The finding of preyed-upon clutches in many nests, including some in nests that appeared to have been abandoned early during construction, suggests that predation while the female is away may be significant. Nests of *M. bracteatus* were also vulnerable to attack by *A. imbecilla*, a mantispid and a specialist predator of spider eggs. Mantispid larvae consumed virtually all the eggs in the nests examined (see also Downes 1985) suggesting that maternal *M. bracteatus*, by laying all their clutches in the one nest, potentially place at risk their entire season's, and perhaps lifetime's, reproductive effort.

Females of *M. bracteatus* may lay all their clutches in one nest because overlying bark on scribbly gum trunks is both sparse and ephemeral, and so nest sites are in short supply. Theory suggests that egg cannibalism and delayed juvenile dispersal may arise because the oviposition sites of females are widely separated from the juvenile habitat (which may be the case in *M. bracteatus*) and that an unknown fitness advantage accrues to females by producing fewer, larger young (Crespi 1992). Alternatively, this delay, and the con-

sequent larger size of juveniles at dispersal, may be a fortuitous outcome of the opportunity to cannibalize siblings (and possibly, the mother) afforded by constraints on nesting sites.

Cannibalism of siblings in the nest is common in many solitary spider species (Krafft 1982) and it also occurs in some species with extended sociality (Evans et al 1995, but see Brach 1975). It has been argued that sociality in spiders evolved in some via an extension of an initial tolerant phase in the egg sac (Avilés 1997). The occurrence of sibling cannibalism in *M. bracteatus* is therefore interesting because it exists alongside a tolerance amongst larger juveniles.

Studies have shown that colonial-living web-building spiders capture more prey than solitary individuals, but that they are also subject to "costs" unique to this way of life, i.e., an increased vulnerability to predators and parasites as the size of the colony increases (see Uetz & Hieber 1997 and references therein). Most social spider species occur in the tropics (Avilés 1997) where numbers of specialist predators and parasitoids are very high (Begon et al. 1996). The occurrence in the solitary maternal social sub-tropical *M. bracteatus* of high rates of nest predation by a specialist mantispid egg predator raises the possibility that high rates of predation or parasitism could be a cause rather than simply a consequence of group-living in spiders.

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RESEARCH NOTE

EGG SACS OF *PITYOHYPHANTES PHRYGIANUS* ARE NOT AFFECTED BY ACID RAIN

Keywords: Air pollution, reproduction, spider embryos

Acidic precipitation is one of the most important air pollution problems today, causing ecological as well as physiological effects on terrestrial and aquatic animals (Newman et al. 1992). However, the effects on terrestrial arthropods are poorly known. In their review of pollution and insects, Heliövaara & Väisänen (1993) found only three studies focussed on the direct effects of acid rain on terrestrial arthropods. In one of the studies, the growth rate of juvenile spiders exposed to simulated acid rain was examined (Gunnarsson & Johnsson 1989). However, earlier stages during development may be exposed to acid rain as well. Spiders deposit their eggs within an egg sac. The sac is a shelter for the eggs and made of spider silk, consisting of protein with alanine and serine as two major components (Foelix 1996). Each developing spider egg is protected by the chorion layer (Foelix 1996). This means that in order to damage the embryonic spiders, the acidic water must penetrate not only the silken egg case, but also the chorionic egg shell.

Here I examine the effects of simulated acid rain on egg sacs of the spruce-living (*Picea abies* (L.)) sheetweb spider *Pityohyphantes phrygianus* (C.L. Koch 1836). In south Sweden, it has a biennial life-cycle. The males mature before the females in late spring (Gunnarsson & Johnsson 1990), and mating takes place in May. In late June, the females start reproducing, placing their egg sacs directly on spruce branches. This means that the egg sacs in most areas of south Sweden are exposed to ambient concentrations of air pollutants, including acid rain, for about three weeks until hatching starts.

Adult females were collected from spruce branches at different sites in coniferous forests 20–40 km east of Göteborg in SW Sweden.

The females were collected at the end of June, when egg production starts. In the laboratory, the females were placed in 0.5 liter plastic vials with spruce twigs. They were fed with vestigial wing fruit flies (*Drosophila melanogaster*) *ad libitum*. The vials were sprayed with tapwater at regular intervals to maintain the humidity. All experiments were performed at room temperature (21–25 °C) and under natural photoperiod.

The females produced a first egg sac, which was attached to a twig or to the inside wall of the vial. The egg sacs were carefully removed and placed individually in 10 ml plastic vials, which were closed with a cotton ball. Approximately 70% of the females produced a second egg sac. All further treatments of the egg sacs were randomized.

Each egg sac, once a day, was gently sprayed with water of a particular acidity, which formed a cover of small drops on the egg sac and the insides of the vials. The spraying was done in a standardized fashion that was similar in all treatment groups. The control group was sprayed with tapwater of pH 7 and the experimental groups with water of pH 4.0 (simulated acid rain; mean of bulk deposition in south Sweden is pH 4.3, see Balsberg Pålsson & Bergkvist 1995), and pH 2.2. The solutions were obtained by using a stock solution of tap water for all treatments. Parts of this stock solution were mixed with diluted sulphuric acid. The pH of the solutions was checked at regular intervals and found to remain constant. However, new solutions were prepared once during the experiment. This experiment is referred to as the “main experiment.”

The egg sacs were checked in two ways. First, spiderlings that had emerged from the egg sac were recorded. If no spiderlings were

observed, the egg sac was opened 25 days after its deposition. Second, the hatching success was established by counting the numbers of hatched spiderlings and dead/undeveloped eggs. In egg sacs where spiderlings emerged spontaneously, the spraying of water was ceased on the day of emergence and all spiderlings and any remaining eggs were checked after another two days.

In the presentation of data, means are given together with their standard deviations. Non-parametric statistical methods were used since non-normality was observed in hatching data and transformation did not change this. All tests were two-tailed.

To provide a comparison with experimental results, egg sac production in a natural population 40 km east of Göteborg was recorded in July. The number of eggs was counted and used for comparison with the experimental situation. Egg sacs from the wild were not used in any experiment. A field-collected egg sac contained, on average, 43.2 ± 15.9 eggs ($n = 17$). However, there was a negative correlation between the collecting date and the number of eggs in the natural population (Spearman rank correlation test; $r_s = -0.589$, $P = 0.019$, $n = 17$). This suggests that females in the wild produced smaller clutches later in the season, possibly because there are fewer eggs in a second egg sac. It is known from other species that females produce fewer eggs in successive egg sacs (Foelix 1996).

The mean number of eggs in an egg sac in the main experiment was 36.4 ± 12.8 ($n = 88$). The egg numbers in the first and second egg sac were similar (Wilcoxon matched-pairs signed-ranks test; $z = -0.74$, $P = 0.46$, $n = 31$), and not correlated (Spearman, $r_s = 0.162$, $P = 0.36$, $n = 31$). Egg production in the laboratory was similar to the natural population (Mann-Whitney U -test; $z = -1.48$, $P = 0.14$, $n_1 = 88$, $n_2 = 17$).

Spiderlings emerged spontaneously from egg sacs sprayed with water of different acidity except for those treated with water of pH 2.2. A comparison of egg sacs with spontaneously emerging spiderlings in the main experiment showed a highly significant difference between the treatments ($\chi^2 = 26.20$, $df = 2$, $P = 0.001$): spiderlings emerged in 72.7% ($n = 33$) of the egg sacs in the control (pH ≈ 7), 65.5% ($n = 29$) in pH 4.0, and 0% ($n = 17$) in pH 2.2.

In the main experiment, the hatching success of the spiderlings in the first and second egg sac was similar within each treatment (Mann-Whitney U -tests; $0.51 < P < 0.75$). Consequently, first and second egg sacs were pooled in the analyses. Comparisons between the treatments (pHs ≈ 7 (control), 4.0 (simulated acid rain), 2.2) showed that the hatching success differed significantly (Kruskal-Wallis one-way ANOVA; $H = 13.43$, $df = 2$, $P = 0.0012$). Multiple comparisons at the 5% level (Siegel & Castellan 1988), showed that the mean hatching rate in pH 2.2 ($13.7\% \pm 17.0\%$, $n = 17$) differed from control ($51.8\% \pm 37.2\%$, $n = 33$) and from simulated acid rain ($43.1\% \pm 38.3\%$, $n = 29$), but there was no difference between the two latter treatments. Pooling the treatments of pH ≈ 7 and 4.0 revealed a negative correlation between the number of eggs in each egg sac and the hatching success (Spearman, $r_s = -0.504$, $P = 0.0001$, $n = 62$). This was, however, not the case in pH 2.2 ($r_s = 0.091$, $P = 0.71$, $n = 17$).

In an additional, small scale experiment one year after the main experiment, treatments with pH ≈ 7 (control), pH 4.0, pH 3.5 and pH 3.0 solutions were performed as in the main experiment. The reason for doing this additional experiment was to examine the effects of another two acidic solutions (pH 3.5 and 3.0), and test for a possible threshold below pH 4.0. This experiment was analyzed separately since it was performed at room temperature, i.e., there were slightly different conditions between years.

In the additional experiment, approximately similar percentages (67–78%) of egg sacs with emerging spiderlings were observed among the groups (pHs ≈ 7 , 4.0, 3.5, and 3.0). The hatching success of spiderlings in the treatments pH ≈ 7 (mean $80.9\% \pm 36.6\%$, $n = 5$), pH 4.0 ($75.5\% \pm 35.2\%$, $n = 8$), pH 3.5 ($83.3\% \pm 31.9\%$, $n = 9$), and pH 3.0 ($68.8\% \pm 54.0\%$, $n = 3$) was similar (Kruskal-Wallis one-way ANOVA; $H = 0.25$, $df = 3$, $P = 0.97$). There was no correlation between the number of eggs in each egg sac and the hatching success (Spearman, $r_s = 0.161$, $P = 0.43$, $n = 25$).

Obviously developing embryos are rather well protected against acid rain since only egg sacs treated with water of pH 2.2 showed a statistically significant deviation from the con-

tol. Examination of the egg sacs suggested that the outside structure of the sacs was affected at this low pH. The silk formed a dense mass of threads, which were glued together but with minute openings in between, in contrast to the loose structure of threads in the unaffected egg sacs. This had two consequences: (1) the hatched spiderlings could not emerge from the egg sac, possibly because they could not find their way out of walls consisting of threads glued together; (2) the hatching of spiderlings was affected negatively, suggesting that acidic water entered the damaged egg sac and reached the developing embryos.

The correlation between egg numbers on hatching success of spiderlings may be an artifact due to disturbance. Removal of egg sacs from the deposition points may have caused unfavorable position changes of eggs within clutches. It is also possible that the water spraying was insufficient to support all eggs in large clutches with enough moisture. In natural populations, the mean hatching success of spiderlings seems to be >90% (pers. obs.). The experimental hatching success was low even in the control, suggesting that the laboratory conditions affected the results, at least in the main experiment. However, the egg numbers per egg sac in the natural population and in the experiment were similar.

The pH of throughfall water in spruce was slightly higher than bulk deposition in south Sweden, averaging 4.3–4.6 (Balsberg Pålsson & Bergkvist 1995). Thus, there is no evidence suggesting that acid rain affects the development of embryos within spider egg sacs, unless under extreme conditions. Similar results were obtained for growing juveniles of *P. phrygianus* (Gunnarsson & Johnsson 1989). In the present system, indirect effects of acid rain are more important. For instance, accelerated needle-loss is causing changes in predator-prey interactions, involving spiders and their predators (Gunnarsson 1995, 1996; Sundberg & Gunnarsson 1994).

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RESEARCH NOTE

WHICH SPERMATHECA IS INSEMINATED BY EACH PALP IN THERAPHOSIDAE SPIDERS?: A STUDY OF *OLIGOXYSTRE ARGENTINENSIS* (ISCHNOCOLINAE)

Keywords: Theraphosid copulation, insertion side, mono-palpectomized males

Which female receptacle is reached by a particular (right or left) palpal organ and how deep the embolus is inserted are unresolved problems in mygalomorph spiders. Despite evidence for the sperm storage function of spermathecae in some haplogyne spiders (including Mygalomorphae) (Coyle et al. 1983), literature dealing with these questions is scarce. The complementarity between male and female genital structures has been, until now, the only useful evidence regarding the lateral correspondence and the depth of insertion in Mygalomorphae (Coyle et al. 1983; Costa & Pérez-Miles 1998) studied both issues using copulations by mono-palpectomized males and consequent histological identification and location of sperm masses in the two spermathecal receptacles.

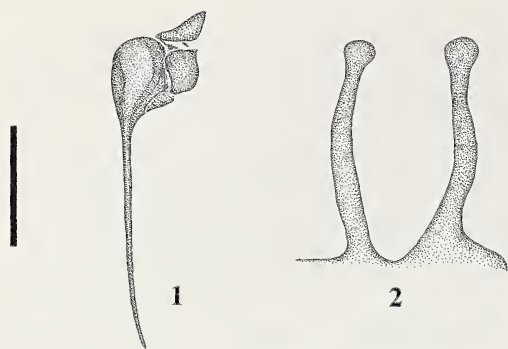
Oligoxystre argentinensis (Mello-Leitão 1941) is a medium-sized theraphosid from temperate South America. Male palpal organs have a very long embolus (Fig. 1). The adult females have, attached to the bursa copulatrix, two separated spermathecal receptacles, each one consisting of a long stalk with a spherical fundus (Fig. 2). Three males and six females of this species were collected in Sierra de las Animas (34°45'S, 55°21'W), Maldonado, Uruguay. They were reared in petri dishes containing moist cotton, and fed mainly with larvae of *Tenebrio* sp. (Coleoptera, Tenebrionidae). Females molted in the laboratory, thus they had empty spermathecae.

The right palpal organ of each male was covered with a drop of paraffin to prevent its use, but the covered palps were autotomized one or two days after manipulation. After a week each male was placed together with a "virgin" female for the first series of copulations. At least a week after these encounters,

each male was placed with another "virgin" female for a second series of copulations. As soon as copulations were finished females were mechanically sacrificed by a cephalothorax puncture, and their spermathecae were immediately removed by dissection. Spermathecae were fixed in paraformaldehyde, impregnated with osmium tetroxide and embedded in araldite. Longitudinal sections were stained with toluidine blue and examined with an optical microscope. Voucher specimens were deposited in the arachnid collection of the Facultad de Ciencias, Montevideo.

In the first series of copulations each male inserted his only palp (the left) 2, 3 and 4 times, respectively. In the second series each of the three males performed two insertions. In the first series two females each had both spermathecal receptacles completely filled with sperm (Fig. 3) (the third specimen, corresponding to the two-insertion copulation, was damaged). In the second series, one female had her left spermathecal receptacle filled with sperm and the right one empty; while in the other two females, both spermathecal receptacles were empty. The only male which had inseminated a female in the second series had performed only two insertions in the first series.

The availability of both filled and empty spermathecal receptacles made it possible for us to study and compare them. We observed in the spermathecal wall the presence of orifices and features that resemble pores and glands as described by De Carlo (1973) in species of *Grammostola* and *Acanthoscurria*. Sections of four sperm-filled receptacles and sections of five empty receptacles were measured (in mm), with an accuracy of 0.01 mm. Mean total width (measured in the middle of



Figures 1, 2.—*Oligoxystre argentinensis*. 1, Left male palpal organ (ventral view); 2, Female spermathecae (ventral view). Scale = 1 mm.

their length) of filled receptacles was $0.30 (\pm 0.00 \text{ SD})$, while empty receptacles measured $0.274 (\pm 0.046 \text{ SD})$. The Student's *t*-test showed significant differences between them ($t = 6.14$, $P < 0.001$). Mean wall width (including inner cuticle and epithelial layer, following De Carlo 1973) showed no significant differences between filled and empty receptacles ($0.125 \pm 0.17 \text{ SD}$ and 0.126 ± 0.17 , respectively). The mean width of the lumen was $0.063 (\pm 0.010 \text{ SD})$ in sperm-filled receptacles, and $0.023 (\pm 0.022 \text{ SD})$ in empty ones. The Student's *t*-test showed significant differences between them ($t = 3.63$, $P < 0.01$).

Results indicate that a given palp is able to inseminate either or both spermathecal receptacles in *O. argentinensis*. Unexpectedly, there is no evidence of morphological or ethological constraints which prevent a palp from delivering sperm to either receptacle. Our findings also suggest that sperm are directly deposited by the embolus deep into the spermathecal receptacles, since females were sacrificed soon after mating and no immediate sperm transfer mechanisms along the spermathecae are known. The increased receptacle lumen width in filled spermathecae resulted from the stretching (expansion) of the spermathecal wall rather than the reduction of wall thickness. Finally, the low insemination level observed in the second series lead us to suspect that these males had difficulties recharging the palpal organs after their first copulations. One



Figure 3.—Longitudinal section of a spermathecal receptacle of *Oligoxystre argentinensis* filled with sperm mass.

possible explanation could be that the absence of one palp disturbed the sperm induction behavior of these males.

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We are grateful to F. Coyle, W.E. Eberhard and B.A. Huber for their critical reading of the manuscript, and to P. Sierwald and J. Berry for the editorial corrections. We thank O. Trujillo-Cenoz, A. Fernandez and G. Casanova (IIBCE) for their technical support.

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Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu. 27, 29, 31, 33, Dorsal views; 28, 30, 32, 34, Proximal views of moveable finger; 27, 28, *A-us x-us*, holotype male; 33, 34, *A-us y-us*, male. Scale = 1.0 mm.

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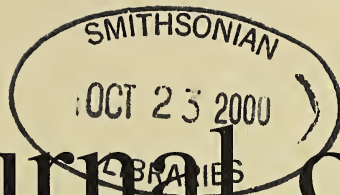
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Cover photo: SEM of cuspule of inner proximal maxilla surface from exuvium of sub-adult *Brachypelma boehmi* (Araneae, Theraphosidae). Greatest width of cuspule=45 μ m. (Photo by Bruce Cutler of the University of Kansas)

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DESCRIPTION OF THE MALE OF *SOSIPPUS PLACIDUS*, WITH NOTES ON THE SUBFAMILY SOSIPPINAE (ARANEAE, LYCOSIDAE)

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ABSTRACT. The male of the Florida funnel-web building wolf spider species *Sosippus placidus* Brady 1972 is described and figured for the first time. Analysis of the male palp's morphological structure reveals that *Sosippus* possesses a median apophysis like other members of the Araneoclada, but which of the three additional tegular apophyses is the conductor cannot be determined at present. The study demonstrates that the palea, the putative key apomorphy of the clade Venoniinae-Allocosinae-Pardosinae-Lycosinae requires further morphological analysis. The genus *Porrmosa* is a close relative of the genus *Sosippus* based on shared characters in the male palp. The ontogeny of the female copulatory organs of *Sosippus* agrees with that of other members in the RTA clade. *Hippasella nitida* Mello-Leitão 1944, placed by Capocasale (1990) in the genus *Sosippus*, is not recognized as a congener.

Keywords: *Porrmosa*, lycosid subfamilies, male palp structure

Members of the North American wolf spider genus *Sosippus* Simon 1888 build rather large funnel-shaped capture webs in shrubs and herbaceous vegetation. The webs are strikingly similar to the "typical" agelenid webs. The web-building habit of *Sosippus* and a few other lycosid genera is frequently cited as "unusual" for the hunting spiders, as Lycosidae are often called (e.g., Gertsch 1949: 194). Simon (1898: 322) placed *Sosippus* and some of the other lycosid genera with long posterior spinnerets in the Hippasae (later subfamily Hippasinae), whereas he assigned *Aulonia* C.L. Koch 1848, which also has long posterior spinnerets, to the Lycosae (later subfamily Lycosinae). Roewer (1959: 7) suggested transferring all lycosid genera with long posterior spinnerets to the Hippasinae. Lehtinen & Hippa (1979: 3) argued that the funnel-web is "simply a plesiomorphic character for a wide group of families within the Amaurobiomorpha," rendering the Hippasinae as defined by Roewer polyphyletic. Citing genitalic characters, they placed *Sosippus* in the Lycosinae.

Dondale (1986: 329) introduced the new lycosid subfamily Sosippinae, containing *Sosippus*, "... *Porrmosa* and its relatives," but did not provide a listing of all genera to be included. He also proposed a new subfamily system for the Lycosidae, placing the Sosip-

pinae as sister taxon to the four other subfamilies, the Venoniinae, Allocosinae, Pardosinae and Lycosinae. Groups and nodes of Dondale's subfamily system are supported exclusively by morphological characters of the male palp. Since the Lycosidae is a species-rich family with considerable morphological diversity of the copulatory organs and the sistergroup to the Lycosidae is not yet known, the characters cited by Dondale require further analysis with regard to polarization (e.g., "loss" of terminal apophysis) and homology status. Zyuzin (1985, 1993) proposed a somewhat different subfamily system for the Lycosidae, stressing the importance of characters derived from the copulatory organs as well. He did not discuss Dondale's proposal of the new subfamily Sosippinae.

In the present study, the male of *S. placidus* is described for the first time, and the structural relationships of the sclerites in the genital bulb are analyzed. Comparison with sclerite and apophyses structure in palps of other lycosid groups will establish testable homology hypotheses required for further phylogenetic analyses of the Lycosidae. The ontogeny of the female organs is also illustrated.

Taxonomic history of the genus.—In the first revision of the genus, Brady (1962: 131) placed the then-known North and Central American *Sosippus* species in two groups: one

group with an eastern North American distribution, including *S. floridanus* Simon 1898, *S. mimus* Chamberlin 1924, and *S. texanus* Brady 1962; and the other group with a western and Central American distribution, including *S. californicus* Simon 1898, *S. mexicanus* Simon 1888, *S. michoacanus* Brady 1962, *S. plutonus* Brady 1962, and *S. agalenoides* Banks 1909. In a subsequent study of the eastern North American species (called *floridanus* species group), Brady (1972) described the additional species, *S. janus* and *S. placidus*. The latter species was based on female specimens alone; and its current known distribution is restricted to Highlands County in central Florida, near Lake Placid. Capocasale (1990) transferred the South American *Hippasella nitida* Mello Leitão 1944 to the genus *Sosippus*.

METHODS

During studies in Florida, the author obtained nine juvenile *S. placidus* specimens from Dr. M. Deyrup, who collected them at Archbold Biological Station near Lake Placid at the original type locality. The specimens were reared in the lab; they built capture webs and took prey readily. Three males matured in April 1987. The molted exoskeletons of all specimens were collected. Exoskeleton sections from between the book lungs were removed from the juvenile and subadult females' molts and mounted ventral side up on SEM stubs. The samples were air-dried and sputter-coated. SEM photographs were taken with several different scanning electron microscopes at the Field Museum and at the National Museum of Natural History (Washington, DC). *Sosippus* specimens of other species were borrowed from institutions listed in the acknowledgments. All measurements are in mm.

In 1994, it was suggested that *S. placidus* be placed on the list of endangered and threatened species (U.S. Dept. of the Interior. Federal Register 59(219): 58982), but this proposal was not adopted (U.S. Dept. of the Interior. Federal Register 61(40)).

Sosippus placidus Brady 1972

Figs. 1–9

Sosippus mimus [in part], -Brady 1962: 156, figs. 34, 35.

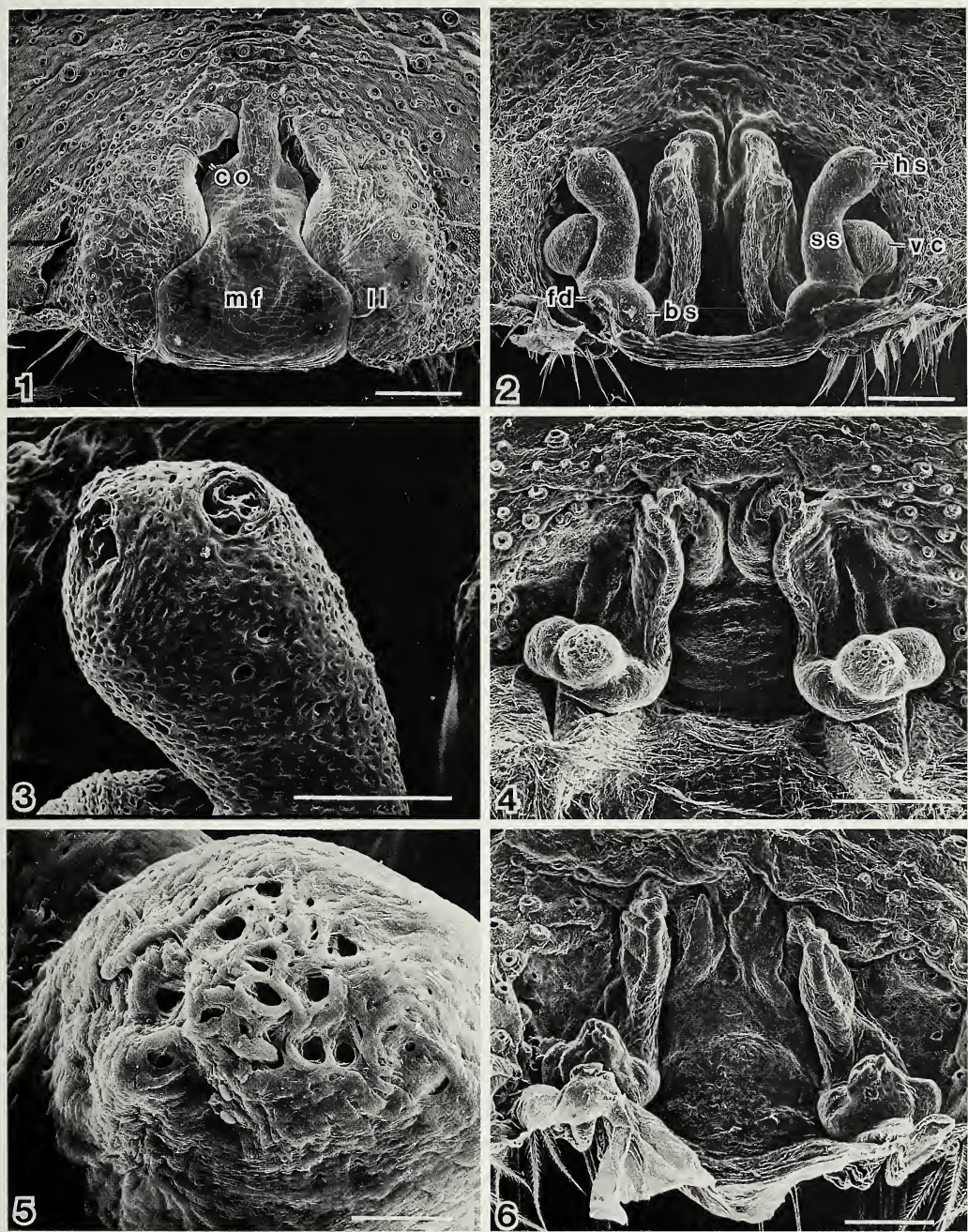
Sosippus placidus Brady 1972: 46, figs. 25–27, 39, map 1. ♀ holotype: USA, Florida, Highlands

County, 6 miles W of Lake Placid, Brady & Tothaker coll.; MCZC. Brignoli 1983: 458.

Diagnosis.—*Sosippus placidus* can be distinguished from all other members of the genus by the bright orange ventral coloration of sternum, legs and abdomen; large adult size (♀ 19–32 mm, ♂ 16–24 mm); and the three retromarginal cheliceral teeth, of which the innermost is twice as large as the other two. *Sosippus texanus* Brady 1962 is very similar to *S. placidus* in body size, number and size ratio of cheliceral teeth and morphology of the copulatory organs, but it lacks the bright orange ventral coloration. Almost the entire middle field of the epigynum (also called septum by other authors) is very broad in *S. texanus* (see Brady 1962, figs. 21, 22), whereas it widens only posteriorly in *S. placidus* (Fig. 1). In the male palp, apophysis *a* is tapered with a round tip in *S. texanus* (see Brady 1962, figs. 37–39), whereas it carries a distinctly swollen tip in *S. placidus* (Fig. 7).

Relationships.—The eastern North American species *S. mimus*, *S. janus*, and *S. floridanus* possess four retromarginal cheliceral teeth (with some individual variation). The remaining species in the genus have three cheliceral teeth; in *S. texanus* and *S. californicus* these have the same size ratio as in *S. placidus* (unknown for the remaining species). Detailed studies into such morphological characters may provide support for the delineation of species groups.

Description.—*Male*: Measurements (3♂): body 16.0–24 long, carapace 6.2–7.5 long, 5.3–7.0 wide; sternum 3.0–4.5 long, 2.1–3.7 wide; labium 0.6–0.9 long, 0.2–0.5 wide. Right leg IV, femur 7.5–10.5 long, patella-tibia 10.0–12.0, metatarsus 10.0–12.5, and tarsus 3.3–6.5; total leg length: 34.0–41.5. Males slightly smaller than females with longer legs than females (see below). Leg formula IV, I–II, III; length: leg IV 34–41.5; legs I and II 30–32; Leg III, 21–25. Spination of legs (see Table 1): spination of femur and patella identical in all species of the genus (with some individual variation); spination of tibia and metatarsus with intraspecific variation especially regarding the dorsal tibial spines on legs III and IV. Color pattern: Carapace orange brown (rust), eye region dark with eyes circled in black; a black thin stripe lining the periphery of the carapace. Chelicerae brownish-



Figures 1-6.—*Sosippus placidus*, female copulatory organs; SEM. 1. External features; *co* = copulatory opening, *ll* = lateral lobe, *mf* = middle field; 2. Internal organs; *bs* = base of the spermatheca, *fd* = fertilization duct, *hs* = head of spermatheca, *ss* = stalk of spermatheca; *vc* = vulval chamber; 3. Head of spermatheca enlarged, showing pores; 4-6. Anlagen of the female copulatory organs, dorsal view, molts. 4. Penultimate instar; 5. Penultimate instar, head of spermatheca enlarged showing pores; 6. Antepenultimate instar. Scale bars: Figs. 1, 2 = 0.2 mm; Figs. 3, 6 = 0.05 mm; Fig. 4 = 0.1 mm; Fig. 5 = 0.001 mm.

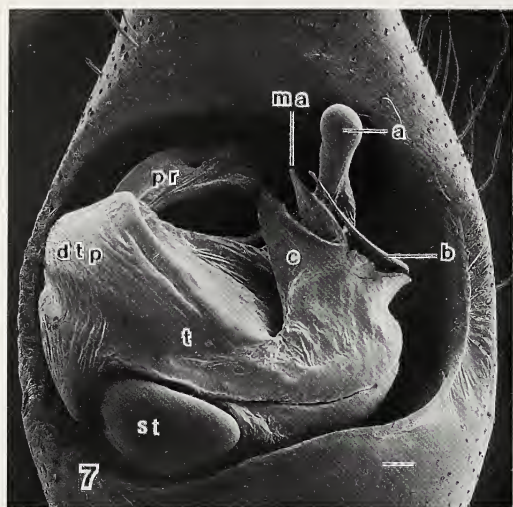


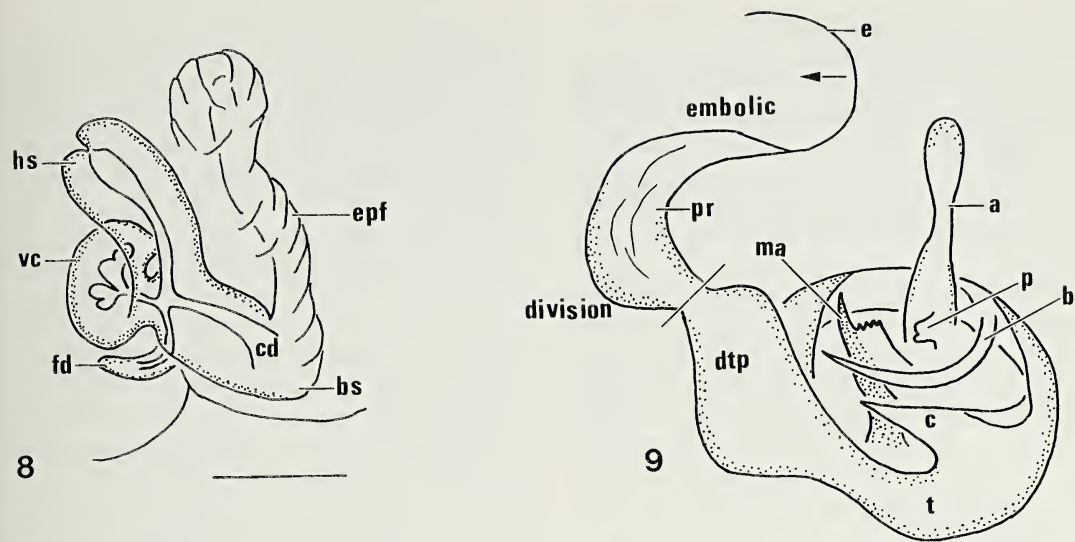
Figure 7.—*Sosippus placidus*, left male palp, ventral view; SEM. Abbreviations: *a*, *b* and *c* = tegular apophyses; *dtp* = distal tegular projection, *ma* = median apophysis, *pr* = palea region, *st* = lunar plate of subtegulum, *t* = tegulum. Scale bar: 0.5 mm.

black; sternum pale orange to yellow (in alcohol); labium and endites darker orange to reddish-black. Ventral surface of abdomen tan to orange, laterally darker orange to red with black hairs; dorsum light brown to tan. Legs brown with alternating light and dark bands; coxae and trochanters bright orange to yellow, covered with white hairs. Palp (Figs. 7, 9): apophysis *a* (labeled conductor by Brady (1962), see discussion below) distinctly swollen and tip sclerotized (Fig. 7).

Female: Measurements (8♀): body 19.0–32.0 long; carapace 6.8–8.4 long, 6.0–7.0 wide; sternum 3.5–4.7 long, 2.4–3.7 wide; labium 0.6–1.1 long, 0.3–0.6 wide. Right leg IV: femur 5.0–8.4 long, patella-tibia 8.4–10.0, metatarsus 4.2–8.7, tarsus 3.3–5.0. Total leg length: 24.0–30.3. Leg formula, spination and color pattern as in male (see also Brady 1972: 47), except for two dorsal rows of five white spots along the axis of the abdomen (see Brady 1972, fig. 39). Epigynum (Fig. 1) with a wide posterior section of the middle field (septum), and large copulatory openings in anterior region of the epigynal folds; internal organs (Figs. 2, 8, and see below) consist of true spermatheca with base, stalk and head, and a kidney-shaped sclerotized chamber (labeled *vc* vulval chamber).

Specimens examined: *Sosippus californicus*: MEXICO: Sonora, San Pedro Bay, 1♀, 17 July 1921, coll. J.C. Chamberlin (paratype of *S. pragmaticus* Chamberlin 1924); CASC. *Sosippus floridanus*: UNITED STATES: Florida, Alachua County, Gainesville, 2♀1♂ (immature), 16 November 1935, coll. W.A. Murrill; MCZC. Alachua County, 1♂, 8 May 1934, coll. A.F. Carr, det. Brady; AMNH. Highland County, Highland Hammock State Park, Sebring, 1♀, 24 March 1938, coll. Gertsch, det. Brady; AMNH. *Sosippus janus*: Florida, Alachua County, NW shore of Lake Lochloosa, 3♀, 10 June 1968, coll. A.R. Brady and J. Toothaker; MCZC. Alachua County, 1♀1♂, 18 April 1935, coll. A.F. Carr; AMNH. *Sosippus mimus*: Florida, Liberty County, Blountstown, 6♂, 17 April 1938, coll. Gertsch; AMNH. Texas, Hidalgo County, Edinburg, 1♀, September–December 1933, coll. Mulaik; MCZC. Florida, Highland County, Lake Placid, 1♀, 1♂ (immature), 1943, coll. M. Cazier, det. Brady; AMNH. Liberty County, Blountstown, 1♂, 4♀ (immature), 17 April 1938, coll. Gertsch, det. Brady; AMNH. *Sosippus placidus*: Florida, Highland County, Lake Placid, Archbold Biological Station, 6♀3♂, September 1986, coll. M. Deyrup; USNM, CASC, FMNH. Highland County, Lake Amiz, 2♀, 25 August 1975, coll. Brach; USNM, MCZC. *Sosippus texanus*: Texas, Aransas County, Goose Island State Park, 2♀1♂, 15 June 1961, coll. A.R. Brady; MCZC. Hidalgo County, Edinburg, 1♀, September–December 1933, coll. Gertsch, det. Brady; AMNH. *Porrimosa harknessi* (Chamberlin 1916): PERU, Huadquina 5000 ft, 1♂ holotype, July 1911, Yale Peruvian Expedition; MCZC.

Structure and ontogeny of the *Sosippus* vulva.—The female copulatory organs develop via the formation of paired longitudinal invaginations, termed epigynal folds (*epf*), above the epigastric furrow (Figs. 4, 6). Such folds have been observed in several families in the RTA-clade *sensu* Coddington & Levi (1991) (see Sadana 1972; Lachmuth et al. 1985; Sierwald 1989). The internal female organs (Fig. 2) consist of the true, tri-partite spermatheca with base (*bs*), stalk (*ss*) and head (*hs*) as identified for many Lycosoidea (Sierwald 1989; Griswold 1993). The head of the true spermatheca is clearly recognizable by its pores on the top (Fig. 3). Attached to the base of the spermatheca is a kidney-shaped, sclerotized chamber (*vc*, Fig. 2; labeled *B* by Brady 1962, fig. 20), whose anterior tip lies ventrally of the stalk of the spermatheca (Fig. 8). The copulatory opening is formed by the elongated epigynal folds; the internal sections of the folds are membranous



Figures 8, 9.—Schematic drawings of copulatory organs. Stippling indicates sclerotized areas, lines indicate membranous sections; 8. Trajectory of ducts in vulva, schematic; abbreviations as in Fig. 2, *cd* = copulatory duct; 9. Sclerites of left *Sosippus* genital bulb in ventral view, schematic; *a*, *b*, *c* = tegular apophyses; *p* = protuberance of apophysis *a*; *dtp* = distal tegular projection, *e* = embolus, *ma* = median apophysis, *pr* = palea region, *t* = tegulum. Embolic division tilted out of original position, arrow indicates direction of tilt.

and rather wide, thus resulting in a wide copulatory opening (Fig. 1). The sclerotized base of the spermatheca is attached to the posterior end of the epigynal folds, enclosing the copulatory duct (Figs. 2, 8). The copulatory duct branches into the duct of the spermathecal stalk and the duct leading into the kidney-

shaped vulval chamber. The fertilization duct branches off from the vulval chamber duct.

Antepenultimate and penultimate molts (Figs. 4–6) possess anlagen of the female organs. The ontogeny of these organs follows the same pattern observed in various Pisauridae (Sierwald 1989) and corresponds closely

Table 1.—Leg spination in *Sosippus placidus*. Abbreviations: 1 = spine normal length, i = short spine, [] = common variation, [variations] = different variations common in this location.

	Femur	Patella	Tibia		Metatarsus	
Leg I dorsal	11 i	0	0		0	
Prolateral	11	1	1	1	1	i [variations]
Retrolateral	iii	1	1	1 [0]	1	i [variations]
Ventral	0	0	[1] 11	11 ii	11 11	i
Leg II dorsal	11 i	0	0 [1 1]		0	
Prolateral	11	1	1	1	1	i [variations]
Retrolateral	iii	1	1	1 [0]	1	i [variations]
Ventral	0	0	11 11	ii	11 11	i
Leg III dorsal	11 i	0	0 [1 1]		0	
Prolateral	11	1	1	1	1 1	i
Retrolateral	iii	1	1	1	1 1	i
Ventral	0	0	11 11	ii	11 11	i
Leg IV dorsal	11 i	0	0 [1 1]		0	
Prolateral	11	1	1	1	1 1	i
Retrolateral	i	1	1	1	1 1	i
Ventral	0	0	11 11	ii	11 11	i

to the one observed in *Lycosa chaperi* Simon 1885 by Sadana (1972). Anlagen are formed by paired longitudinal invaginations, with the future head of the spermatheca recognizable in early instars by its pores (penultimate anlage, Figs. 4, 5; antepenultimate anlage, Fig. 6.). In the penultimate anlage (Fig. 4) the kidney-shaped vulval chamber is already recognizable.

Structural analysis of the *Sosippus* palp.—The tegulum of the *Sosippus* genital bulb is ring-shaped (see Figs. 7, 9) as in many other lycosoids and agrees in its basic structure with the pisaurid palp (see Sierwald 1990; fig. 2). The sperm duct enters the tegulum dorsally, runs retrolaterally and turns into the ventral section of the tegular ring.

Brady's (1962: fig. 36) figure of a partially inflated *S. californicus* palp labels a median apophysis, conductor, basal haematodocha, lateral apophysis of conductor, mesal apophysis of tegulum, the tegulum, and the embolus. The tegulum appears to carry four conspicuous apophyses labeled here *a*, *b*, *c* and the median apophysis *ma* (Figs. 7, 9). Apophyses *a* and *b* originate from the dorsal section of the tegular ring. Apophysis *a* (labeled conductor by Brady 1962) is long, slender and finger-shaped. At its base it carries a small bilobed fleshy protuberance *p*, which is not visible in the unexpanded bulb. Apophysis *b* (labeled lateral apophysis of conductor by Brady) originates also in the dorsal section of the tegulum next to apophysis *a*. Apophysis *b* is long and sickle-shaped and lies transversely on the ventral surface in the unexpanded bulb. Apophysis *c* (not labeled but figured by Brady 1962 in fig. 36) originates from the ventral section of the bulb as an outgrowth of the tegular wall and is broad and flat. This apophysis is a thin, very translucent, triangular-shaped lamella, which may be difficult to discern under light microscopy. It is unclear at this point if any of these apophyses is a homologue to the pisaurid conductor.

The fourth apophysis arises from the membranous center of the tegular ring and is most likely the homologue of the median apophysis *ma* (labeled mesal apophysis of tegulum by Brady 1962 in fig. 36; the identity of the part he labeled median apophysis is unclear). It is strongly sclerotized; and its dorsal rim is attached to a fringed lamella (Fig. 9), which lies in the notch below protuberance *p* in the non-

inflated bulb (see Dondale 1986, fig. 2). The elongated tips of the sickle-shaped apophysis *b*, the median apophysis and apophysis *c* point in the same direction in the non-inflated bulb, with the tip of the embolus sandwiched between the median apophysis and apophysis *b*.

The section of the tegulum preceding the embolic division becomes very broad and strongly sclerotized (located prolaterally in the non-inflated bulb directly above the lunar plate of the subtegulum, Fig. 7) and corresponds to the distal tegular projection (*dtp*) in the pisaurid palp. The embolic division is connected to the tegulum by a rather narrow, mostly membranous stalk. In the unexpanded palp, this stalk is bent dorsally and retrolaterally, bringing the embolic division over the tegulum, with the tip of the embolus pointing prolaterally. The base of the embolic division is a wide sac, its walls consisting of partially sclerotized and partially membranous sections. The location of this large sac in the embolic division indicates that it is most likely homologous to the basal membranous tube and the distal sclerotized tube of the pisaurid bulb (see Sierwald 1990: fig. 3) and to the palea of other lycosids (labeled palea region (*pr*) in Figs. 7, 9). The embolus is spine-like, thin, curved and rather short, describing an incomplete loop. In *Sosippus* the embolic division carries no apophyses as they occur in other lycosids.

This study confirms the presence of the median apophysis in the *Sosippus* palp as it has been proposed for the Araneoclada (see Codrington 1990: 10; Sierwald 1990: 44). However, the status of the "conductor" in the *Sosippus* palp is unclear at this point. The conductor, as an outgrowth of the tegular wall, can be found in various families of the Araneoclada (e.g., Anyphaenidae, Pisauridae, Amaurobiidae, Psecridae, Araneidae and others). In the *Sosippus* palp, there are three tegular outgrowths (apophyses *a*, *b*, and *c*), each of which may represent the homologue of the Araneoclada conductor. The other two then represent evolutionary novelties.

The long finger-shaped apophysis *a* is shared by all members of the genus and represents a synapomorphy for *Sosippus* (see Brady 1962, figs. 34–47). Figures of the male palp of *Hippasella nitida* Mello-Leitão 1944 (Capocasale 1990: figs. 12, 13, Mello-Leitão 1944, fig. 32) indicate that this species does

not possess the finger-shaped apophysis, and as far as the figures can be interpreted, its palps have no close similarity with the *Sosippus* palp in general. In addition, Mello-Leitão's description (1944: 343) of the size ratio of the eyes (anterior eyes larger than posterior eyes in *H. nitida*) exclude this species from the genus *Sosippus* (posterior median eyes distinctly larger than anterior eyes in *Sosippus*).

Sosippus shares characters with *Porrimosa* Roewer 1960 (Brady 1962, fig. 33; Capocasale 1982, figs. 6–10). The embolic division is similar, consisting of a sac tilted dorsally and retrolaterally and a short, spine-like embolus, whose tip is sandwiched between the strongly sclerotized apophysis *b* and the tip of the median apophysis in the unexpanded palp. The median apophysis is smaller and less strongly sclerotized in *Porrimosa* than in *Sosippus*. Apophysis *a* is present, but it is short, broad and forms a hump (not long and finger-like, labeled conductor in Capocasale 1982, figs. 6–10). Apophysis *c* is represented by a low ridge arising from the ventral section of the tegulum. The shared characters in the palps of both genera support the close relationship of both genera as mentioned by Dondale.

DISCUSSION

Dondale's subfamily proposal forms a valuable starting point for the analysis of the lycosid interrelationship. The characters Dondale employed for his analysis of lycosid subfamilies will require further analyses of the respective palpal structures and additional, independent character systems should be included. According to his proposal the characters "terminal apophysis lost, tegular groove functioning as a conductor," and "embolus laying in a cluster of tegular apophyses" are apomorphies for the *Sosippinae*. Since the sister-group of the *Lycosidae* is not known yet, it is unclear at this point whether the absence of the terminal apophysis in the *Sosippus* palp represents a synapomorphy or is simply the plesiomorphic condition. The present study demonstrates that the "cluster of tegular apophyses" requires further detailed study in other lycosid groups to develop homology hypotheses, especially to clarify the presence or absence of the *Araneoclada* conductor. The character "tegular groove functioning as a

conductor" cannot be evaluated at this point since the actual function of various parts of the palp is unclear (see Zyuzin 1985, 1993 for a detailed discussion). The character "palea developed," the putative key apomorphy for the taxon *Venoniinae-Allocosinae-Pardosinae-Lycosinae*, equally requires further refinement, since it was demonstrated here that the large membranous sac at the base of the embolus in *Sosippus* consists of sclerotized and membranous parts with similarity to the developed palea in other lycosids. A detailed study of the palea morphology will provide further insight into this putative key apomorphy for other lycosid groups.

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IRACEMA CABOCLA NEW GENUS AND SPECIES OF A THERAPHOSID SPIDER FROM AMAZONIC BRAZIL (ARANEAE, THERAPHOSINAE)

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ABSTRACT. The new genus *Iracema* (Araneae, Theraphosidae, Theraphosinae) comprising the only species *Iracema cabocla*, from the Amazonic state of Roraima, Brazil, is described. The cladistic relationships of this genus within the Theraphosinae are analyzed.

Keywords: Theraphosid phylogeny, Amazonic spider, systematics

Theraphosidae is the most diverse family of the Mygalomorphae, comprising around 80 genera and 800 known species (Coddington & Levi 1991). The subfamily Theraphosinae only occurs in the New World, mainly in the Neotropics, and has been revised recently by Pérez-Miles (1992, 1998) and Pérez-Miles et al. (1996). Following the reasoning of Coddington & Levi (1991) that one third of all spider genera occur in the Neotropics and only 20% of world fauna is described, a large number of Theraphosinae taxa are expected to be discovered, especially considering the poor knowledge of the group. Examining the spider collection of the INPA (National Institute for Amazonic Research, Manaus, Brazil) four specimens of Theraphosidae from Maracá, Roraima, Brazil, were found. These spiders did not fit with any known theraphosid genus, suggesting that they represent a new genus. The study of these spiders showed that they share the main synapomorphies of the Theraphosinae: extended subtegulum, keel on palpal bulbs, theraphosine types of urticating hairs and unilobular spermathecae, which encouraged me to place this new genus within this subfamily. The addition of *Iracema* to a previous cladistic analysis showed that it would be the sister group of *Cyriocosmus* Simon 1903.

METHODS

Abbreviations: AME = anterior median eyes, ALE = anterior lateral eyes, PME = posterior median eyes, PLE = posterior lateral eyes, OQ = ocular quadrangle (including lateral eyes), d = dorsal; p = prolateral, r =

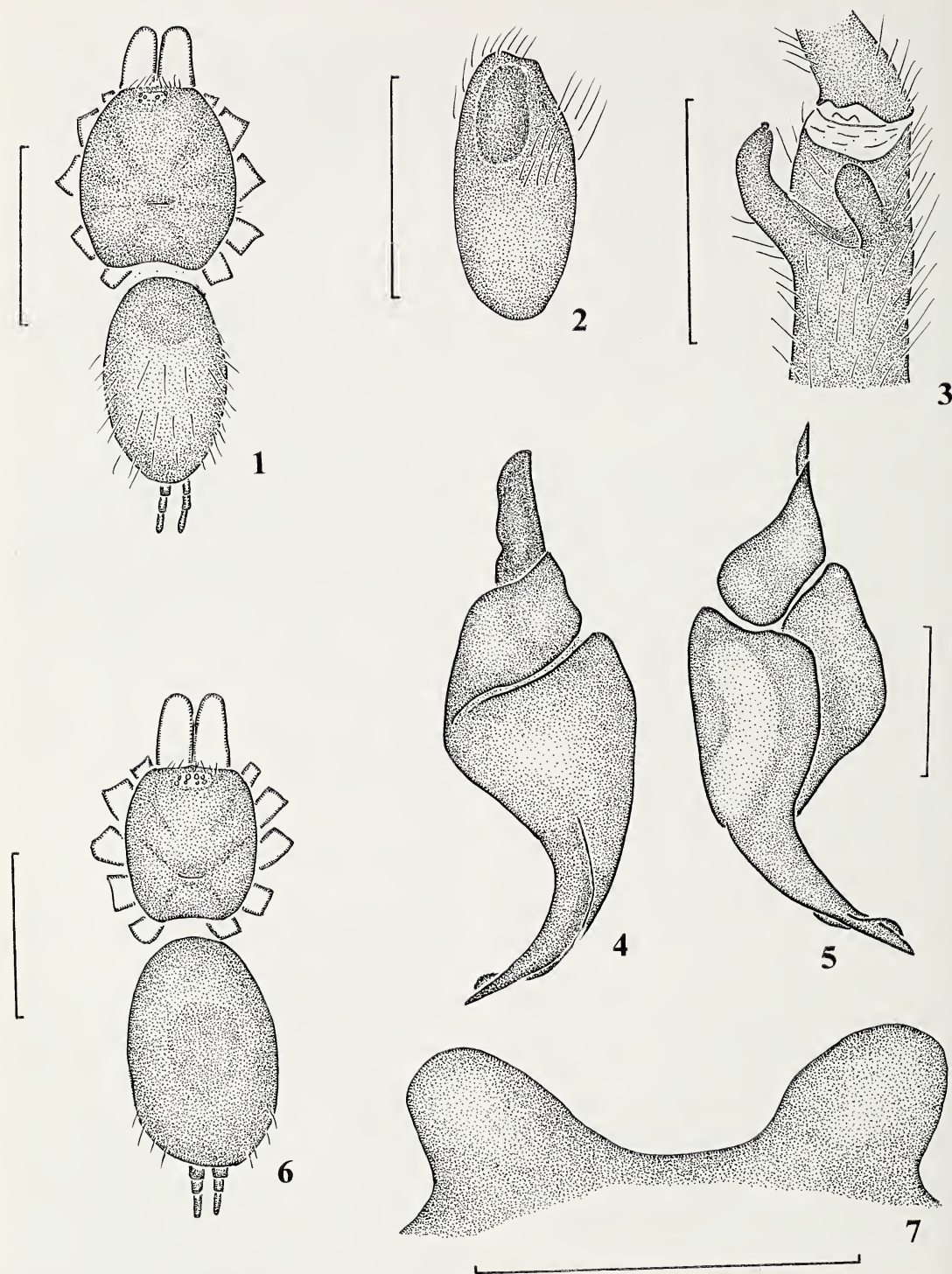
retrolateral, v = ventral; INPA (Instituto Nacional de Pesquisas Amazônicas). All measurements are in mm and were taken using an ocular micrometer. Drawings were made with a camera lucida. Cladistic analysis was based on the previous matrix of Theraphosinae genera (Pérez-Miles 1998, Pérez-Miles et al. 1996) using the Pee-Wee (version 2.5.1) program, developed by Goloboff (1993); multi-state characters are considered as additive because they are part of logically ordered transformation series or morphoclines. Other cladistic techniques follows Pérez-Miles et al. (1996).

***Iracema* new genus**

Type species. *Iracema cabocla* new species.

Etymology.—*Iracema* (feminine) is an anagram of America and the title of the most famous novel of the Brazilian writer José de Alencar, which describes the destruction and oppression of native Amazonic people through contact with civilization.

Diagnosis.—*Iracema* differs from most theraphosid genera in the presence of a process in the retrolateral face of male palpal tibia. Additionally differs from several genera of Theraphosinae in the presence of Type IV urticating hairs and in the very reduced number of labial cuspules. Females lack Type III urticating hairs which are present in males. *Iracema* differs from *Cyriocosmus* in the palpal organ by lacking a paraembolic apophysis and in the spermathecae by the lack of a spiral neck and a caliciform fundus. *Iracema* differs



Figures 1-7.—*Iracema cabocla* new species. 1-5, Holotype male from Brazil, Roraima, Maracá. 1, Dorsal view (scale = 10 mm); 2, Right palpal tibia showing the retrolateral process (scale = 5 mm); 3, Right tibia I, distal portion showing the prolateral tibial apophysis (scale 5 mm); 4, Left palpal organ, prolateral view (scale = 1 mm); 5, Left palpal organ, retrolateral view (scale = 1 mm). 6, 7, Paratype female from Brazil, Roraima, Maracá. 6, Dorsal view (scale = 10 mm); 7, Spermathecae, ventral view (scale = 1 mm).

Table 1.—*Iracema cabocla* new species. Male holotype and (male paratype), length of leg and palpal segments.

	I	II	III	IV	Palp
Femur	10.8 (10.3)	9.5 (8.8)	8.5 (8.0)	11.2 (10.5)	5.7 (5.7)
Patella	5.0 (5.0)	4.7 (4.7)	4.0 (4.0)	4.7 (4.5)	3.3 (3.6)
Tibia	9.2 (9.3)	7.2 (7.0)	6.5 (6.2)	9.3 (8.8)	5.3 (4.8)
Metatarsus	8.2 (7.8)	7.8 (7.6)	8.6 (8.8)	12.5 (12.0)	—
Tarsus	4.8 (5.2)	5.0 (4.5)	5.0 (4.6)	5.4 (5.5)	1.9 (2.0)

from *Grammostola* Simon 1892 by the absence of stridulatory hairs and from *Plesiopelma* Pocock 1901 by the absence of a nodule on the male metatarsus I. The palpal organ of *Iracema* differs from that of *Homoeomma* Ausserer 1871 by the absence of a digitiform apophysis and from that of *Paraphysa* Simon 1892 by the presence of a process on the retrolateral face of palpal tibia. It also differs from *Paraphysa* by the very reduced number of labial cuspules (3, being more than 10 in *Paraphysa*) and by the divided tarsal scopulae. This character was seriously questioned by Pérez-Miles (1994) because it could mainly reflect differences in size. All generic characters are coded in Table 3.

Iracema cabocla new species

Figs. 1–7; Tables 1–2

Types.—Holotype male, from Maracá, Roraima Brazil, 18 July 1987 (Steve Bowles in pit-fall trap). Paratypes: 24 July 1987 (Steve Bowles in pit-fall traps), 1♂2♀ from the same locality of the holotype. All specimens are deposited in the collection of the INPA, Manaus, Brazil.

Etymology.—The specific epithet is a noun in apposition from the Portuguese feminine word “cabocla” which refers to the people (women) from the Amazonic forests. Traditionally it refers to the de-tribalized Indians and diverse racial mixture with Indian blood.

Diagnosis.—The diagnostic generic characters of this monotypic genus can also be used to recognize the species *Iracema cabocla*.

Description.—*Male:* (holotype). Total length, not including chelicerae nor spinnerets 25.6; carapace length 11.2, width 10.33. Anterior eye row slightly procurved, posterior slightly recurved. Eyes sizes and interdistances: AME 0.38, ALE 0.43, PME 0.25, PLE 0.30, AME-AME 0.25, AME-ALE 0.20, PME-PME 0.82, PME-PLE 0.05, ALE-PLE 0.20, OQ length 0.9, width 1.7, clypeus 0.25. Fovea transverse, straight, width 1.7. Labium length 1.4, width 1.9 with 3 cuspules, maxillae with 66 cuspules. Sternum length 4.9, post-sternal sigilla oval, submarginal. Chelicerae with 9 teeth on the promargin (5 proximal of them smaller). Tarsi I-IV densely scopulated, scopulae divided by a stripe of longer, thicker setae; this stripe is narrow in forelegs to wide in hindlegs. Metatarsi I and II scopulate on distal half, III apically scopulate, IV ascopulate. Palpal tibia with a process on the retrolateral face in distal portion (Fig. 2); ventrally two fields of spiniform hairs present (prolateral and retrolateral). Tibia I with prolateroventral, distal double apophysis (Fig. 3). Flexion of metatarsus I between tibial apophysis. Palpal organ piriform, as in Figs. 4–5. Length of leg and palpal segments given in

Table 2.—*Iracema cabocla* new species. Female paratypes (described), length of leg and palpal segments.

	I	II	III	IV	Palp
Femur	6.5 (6.7)	5.7 (5.7)	5.1 (5.3)	7.2 (7.1)	4.9 (4.9)
Patella	4.0 (4.0)	3.4 (3.5)	3.1 (3.3)	3.5 (3.8)	2.9 (2.7)
Tibia	5.3 (5.2)	4.2 (4.2)	3.7 (4.0)	5.7 (5.8)	3.3 (3.5)
Metatarsus	4.2 (4.1)	4.2 (4.0)	4.6 (4.7)	7.3 (7.6)	—
Tarsus	2.8 (2.9)	2.7 (2.9)	3.1 (3.0)	3.4 (3.5)	3.5 (3.5)

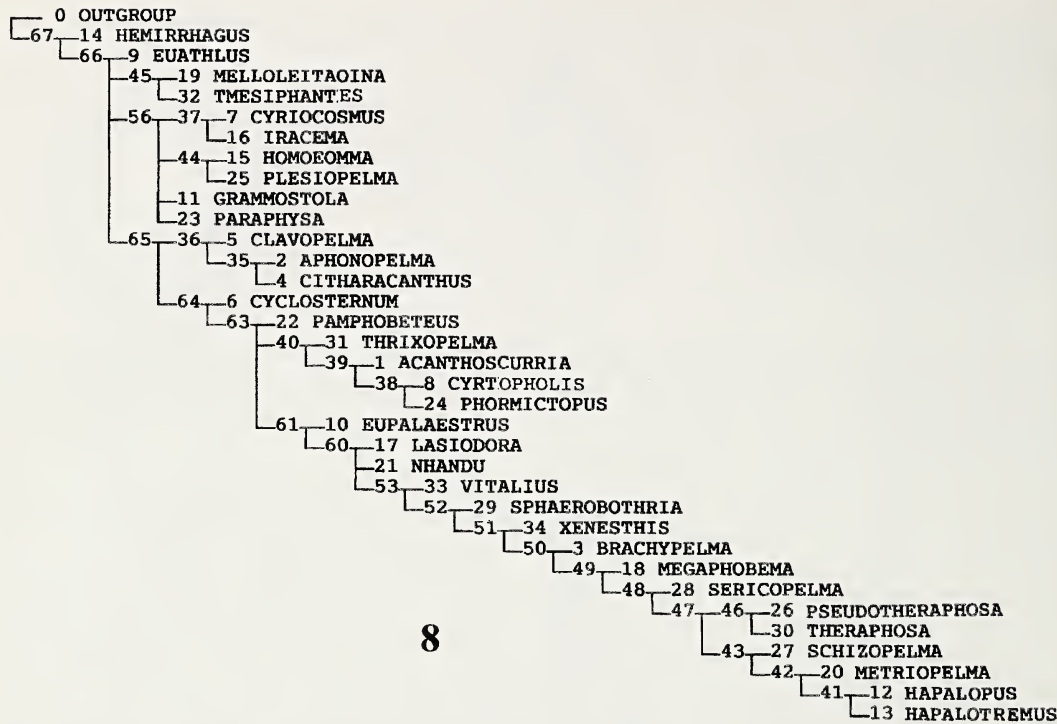


Figure 8.—Tree of genera of Theraphosinae, including *Iracema* new genus (fit 128.0, 80 steps).

Table 1. Femur III swollen. Spination: Femora I-IV and palp I 2P; II 2P; III 3R; IV 1R; Palp 1P. Patellae I-IV and palp 0. Tibiae I 2P, 2V; II 2P, 6V, 1R; III 2P, 4V, 2R; IV 4P, 4V, 2R, Palp 2P. Metatarsi I 1V; II 1P, 5V, 1R; III 5P, 3-4V, 2R, 2D; IV 7P, 4V, 6R, 0-1D. Tarsi I-IV without spines. Color: Cephalothorax reddish-brown; legs and abdomen dark brown. Types III and IV urticating hairs present.

Female: (paratype). Total length, not including chelicerae nor spinnerets 23.5. Cephalothorax length 9.5, width 8.5. Anterior eye row straight to slightly procurved, posterior row slightly recurved. Eye sizes and interdistances: AME 0.40, ALE 0.45, PME 0.23, PLE 0.25, AME-AME 0.20, AME-ALE 0.10, PME-PME 0.78, PME-PLE 0.05, ALE-PLE 0.15, OQ length 0.7 width 1.3, clypeus 0.13. Fovea procurved width 2.0. Labium length 1.50, width 1.95 with 3 cuspules, maxillae with 90 cuspules. Sternum length 4.3, post-sternal sigilla oval, narrow, submarginal. Chelicerae with 9 teeth on the promargin (4 of them proximal, smaller). Tarsi densely scopulate, scopulae divided by a stripe of longer, thicker setae; this stripe is narrow in forelegs to wide in hindlegs. Metatarsi I and II scop-

ulate on distal half, III apically scopulate, IV ascopulate. Length of leg and palpal segments in Table 2. Spination: Femora I-IV and palp, I 1P; II 1P; III 1P, 1D, IV 1D; palp 1P. Patellae I-IV and palp 0. Tibiae I-IV and palp, I 3V; II 1P, 3V; III 2P, 3V, 2R; IV 2V, 1R; palp 1P, 3V. Metatarsi I-IV, I 4V, II 2P, 4V, 1D; III 2P, 4V, 2R; IV 2P, 8V, 5R, 2D. Tarsi I-IV and palp 0. Cephalothorax and legs light reddish-brown, abdomen grey-brown. Only Type IV urticating hairs present. Spermathecae with two receptacles only partly fused (Fig. 7).

Distribution.—*Iracema cabocla* is only known from the type locality, Maracá, Roraima, Brazil, with no further information available.

Cladistic relationships.—Including *Iracema* in the matrix of Pérez-Miles et al. (1996: 37, table 2) modified in the analysis of Pérez-Miles 1998a (Table 3); the most parsimonious tree of total fit 128.0 (43%) and 83 steps was found (Fig. 8), in which *Iracema* was resolved as the sister group to *Cyriocosmus*. Both share the retrolateral process on the palpal tibia (Pérez-Miles 1998b).

List of synapomorphies.—*Acanthoscurria*: char 4: 1 → 2, char 6: 0 → 1; *Brachy-*

Table 3.—Character matrix of genera of Theraphosinae. Characters and (states) as follow: 0 Apical region of palpal bulb: subcylindrical (0), subconical (1), concave-convex (2). 1 Relative width of sclerites II+III of bulb: narrow (less than 10% of length) (0), wide (1). 2 Paraembolic apophysis: absent (0), present (1). 3 Bulbal keels: smooth (0), serrated (1). 4 Bulbal keels: two subequal (0), two unequal (1). 5 Subtegulum: not extended (0), large extended (1). 6 Male tibial apophysis (leg I): double (0), one (1), absent (2). 7 Digitiform apophysis of bulb: absent (0), present (1). 8 Metatarsus I of male: without basal process (0), with basal process (1). 9 Male palpal tibia: without retrolateral process (0), with retrolateral process (1). 10 Male palpal tibia: without retrolateral cluster of spines (0), with retrolateral cluster of spines (1). 11 Male palpal tibia without prolateral process (0), with prolateral process (1). 12 Flexion of metatarsus I (males): on outer side of tibial spurs (0), between tibial spurs (1). 13 Spermathecae: with two receptacles separated or only partly fused (0), widely fused (1), single semicircular receptacle (2), single oval receptacle (3). 14 Spermathecae multilobular in each side (0), unilobular at least in each side (1). 15 Femur III: not incrassate (0), incrassate (1). 16 Tibia IV: not incrassate (0), incrassate (1). 17 Femur IV: without retrolateral scapula (0), with retrolateral scapula (1). 18 Urticating hairs type I: absent (0), present (1). 19 Urticating hairs type III absent (0), present (1). 20 Urticating hairs type IV: absent (0), present (1). 21 Trochanteral "stridulatory" hairs: absent (0), present (1). 22 Coxal "stridulatory" hairs: absent (0), present (1). 23 Coxal spinules: absent (0), present (1). 24 Labial cuspules: numerous (more than 15) (0), few or none (0). 25 Fovea: normal (0), with spheroid process (1). 26 Metatarsus I of males: normal (0), strongly curved (1). 27 Urticating hairs on prolateral palpal femur: absent (0), present (1). 28. Urticating hairs type VI: absent (0), present (1). 29 Coxae: normal (0), retrolaterally extended (1).

[illegible]

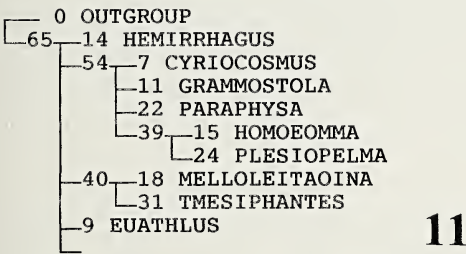
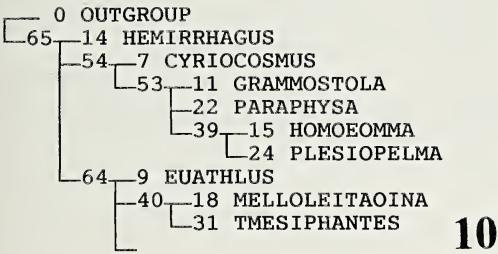
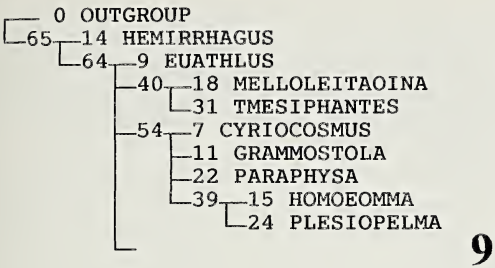
Table 3.—Extended.

	2														
	5	6	7	8	9	0	1	2	3	4	5	6	7	8	9
OUTGROUP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
<i>Acanthoscurria</i>	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0
<i>Aphonopelma</i>	?	0	0	1	0	0	0	0	1	0	0	0	0	0	0
<i>Brachypelma</i>	0	0	0	1	1	0	0	0	0	0	0	0	0	0	0
<i>Citharacanthus</i>	0	0	0	1	0	0	1	0	1	0	0	0	0	0	0
<i>Clavopelma</i>	0	0	0	1	1	0	0	0	1	0	0	0	0	0	0
<i>Cyclosternum</i>	0	0	0	?	1	0	0	0	0	0	0	0	0	0	0
<i>Cyriocosmus</i>	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
<i>Cyrtopholis</i>	0	0	1	1	0	0	1	0	?	0	0	0	0	0	0
<i>Euathlus</i>	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Eupalaestrus</i>	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Grammostola</i>	0	0	0	0	1	1	0	1	0	0	0	0	0	0	0
<i>Hapalopus</i>	0	0	0	0	1	0	0	0	0	0	0	1	0	0	0
<i>Hapalotremus</i>	0	0	0	0	1	0	0	0	0	1	0	1	0	0	0
<i>Hemirrhagus</i>	0	0	0	0	0	0	0	?	0	0	0	?	0	1	1
<i>Homoeomma</i>	0	0	0	0	1	1	0	0	0	0	0	?	0	0	0
<i>Iracema</i>	1	0	0	0	1	1	0	0	0	1	0	0	0	0	0
<i>Lasiadora</i>	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0
<i>Megaphobema</i>	1	0	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Melloleitaoina</i>	1	0	0	0	1	0	0	0	0	1	0	0	0	0	0
<i>Metriopelma</i>	?	0	0	?	?	?	0	0	0	0	0	0	0	0	0
<i>Nhandu</i>	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Pamphobeteus</i>	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Paraphysa</i>	0	0	0	0	1	1	0	0	0	?	0	0	0	0	0
<i>Phormictopus</i>	0	0	?	1	0	0	1	1	0	0	0	0	0	0	0
<i>Plesiopelma</i>	0	0	0	0	1	1	0	0	0	0	0	0	0	0	0
<i>Pseudotheraphosa</i>	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
<i>Schizopelma</i>	0	0	1	0	1	0	0	0	0	0	0	0	0	0	0
<i>Sericopelma</i>	0	0	1	1	1	0	0	0	0	0	0	0	0	0	0
<i>Sphaerobothria</i>	?	0	0	1	0	0	1	0	0	0	1	0	0	0	0
<i>Theraphosa</i>	0	0	1	0	1	0	0	1	0	0	0	0	0	0	0
<i>Thrixopelma</i>	0	0	1	?	?	?	0	1	1	0	0	0	?	0	0
<i>Tmesiphantes</i>	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0
<i>Vitalius</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0
<i>Xenesthis</i>	0	0	1	1	0	0	0	0	0	0	0	0	0	0	0

pelma: char 17: 1 → 0; *Citharacanthus*: char 12: 0 → 1; char 21: 0 → 1; *Cyriocosmus*: char 2: 0 → 1, char 10: 0 → 1, char 19: 1 → 0; *Cyrtopholis*: char 11: 0 → 1; *Eupalaestrus*: char 15: 0 → 1, char 16: 0 → 1; *Grammostola*: char 22: 0 → 1; *Hapalopus*: char 10: 0 → 1; *Hapalotremus*: char 0: 1 → 0, char 1: 1 → 0, char 4: 2 → 1, char 24: 0 → 1; *Hemirrhagus*: char 28: 0 → 1, char 29: 0 → 1; *Homoeomma*: char 3: 0 → 1, char 7: 0 → 1; *Iracema*: char 4: 1 → 0, char 12: 0 → 1, char 15: 0 → 1, char 24: 0 → 1; *Lasiadora*: char 22: 0 → 1; *Megaphobema*: char 15: 0 → 1; *Melloleitaoina*: char 24: 0 → 1; *Metriopelma*: char 6: 1 → 2; *Nhandu*: char 6: 0 → 2; *Pamphobeteus*: char 0: 1 → 2, char 12: 0 → 1; *Phor-*

mictopus: char 0: 1 → 2, char 22: 0 → 1; *Pseudotheraphosa*: char 6: 1 → 0; *Sericopelma*: char 6: 1 → 2; *Sphaerobothria*: char 17: 1 → 0, char 21: 0 → 1, char 25: 0 → 1; *Theraphosa*: char 6: 1 → 2; *Thrixopelma*: char 22: 0 → 1, char 23: 0 → 1; *Xenesthis*: char 12: 0 → 1.

Node 35: char 19: 1 → 0; Node 36: char 23: 0 → 1; Node 37: char 9: 0 → 1; Node 38: char 19: 1 → 0; Node 39: char 21: 0 → 1; Node 40: char 9: 0 → 1; Node 41: char 6: 1 → 0, char 26: 0 → 1; Node 42: char 17: 1 → 0; Node 43: char 0: 2 → 1, char 4: 3 → 2; Node 44: char 8: 0 → 1, char 12: 0 → 1; Node 45: char 15: 0 → 1; Node 46: char 22: 0 → 1; Node 47: char 4: 4 → 3, char 18: 1 → 0;



Figures 9–11.—Alternative resolutions of node 65 of three trees of maximum fit, from the matrix of Pérez-Miles 1998 (unpublished). Node 54 includes genera which share the apomorphic presence of Type IV urticating hairs.

Node 48: char 6: 0 → 1; Node 49: char 13: 1 → 2; Node 50: char 4: 3 → 4, char 19: 0 → 1; Node 51: char 3: 1 → 0; Node 52: char 0: 1 → 2, char 4: 2 → 3; Node 53: char 19: 1 → 0; Node 56: char 20: 0 → 1; Node 60: char 4: 1 → 2, char 13: 0 → 1; Node 61: char 3: 0 → 1; Node 63: char 17: 0 → 1; Node 64: char 0: 0 → 1, char 1: 0 → 1; Node 65: char 18: 0 → 1; Node 66: char 19: 0 → 1; Node 67: char 14: 0 → 1.

DISCUSSION

Iracema is included in Theraphosinae by sharing the synapomorphies of the subfamily. In the cladogram (Fig. 8) *Iracema* was related with the node 56 which includes the group of genera of node 43 in the cladogram of Pérez-Miles et al. (1996: 43, fig. 2). In both trees

these nodes relate *Cyriocosmus*, *Grammostola*, *Paraphysa*, *Homoeomma* and *Plesiopelma* based on the synapomorphic presence of Type IV urticating hairs, also present in *Iracema*. The sexual dimorphism of *Iracema* with respect to the presence of urticating hairs is remarkable; the male has types III and IV while female has only type IV. Recently Bertani (1997) found that in several theraphosid species the males have types I and III urticating hairs while females have only type I. The study of juveniles and the ontogeny of urticating hair types in these species seems to be crucial in determining if Types I and III are lost in females or gained by males during development. This fact has ecological implications related to adult life strategies, mainly relating to theraphosid males being more errant than females. Also, this kind of study could enlighten the phylogenetic aspects of these important characters as well as the possible different functions of different hair types.

The presence of a process in the retrolateral face of palpal tibiae in *Iracema*, somewhat resembles the process of *Cyriocosmus* indicated by Pérez-Miles (1998b), but in the latter genus the process includes a field of spines absent in *Iracema*. This process is also present in other genera group which lack Type IV hairs: *Acanthoscurria* Ausserer 1871, *Cyrtopholis* Simon 1892 and *Phormictopus* Pocock 1901. Another striking character of *Iracema* is the extreme reduction of labial cusps found only in other two theraphosid genera: *Hapalotremus* Simon 1903 and *Hapalopus* Ausserer 1875 (the last without labial cusps); these genera are far from *Iracema* considering other characters (Table 3). They also lack Type IV urticating hairs.

In a previous analysis of the Theraphosinae, Pérez-Miles (1998) obtained three trees of maximum fit (131.5 and 79 steps). These trees show differences in the internal relationships of the node involving genera with Type IV urticating hairs (Figs. 9–11). The present cladistic analysis resulted in only one tree which is better resolved with the inclusion of *Iracema*.

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RESPIRATORY SYSTEM MORPHOLOGY AND THE PHYLOGENY OF HAPLOGYNE SPIDERS (ARANEAE, ARANEOMORPHAE)

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ABSTRACT. The morphology of the respiratory system of basal araneomorph spiders, the Haplogynae and of Entelegynae with female haplogyne genitalia, is reviewed. The homology of cuticular respiratory structures is discussed in light of evidence from abdominal muscles and ontogeny. Ten morphological characters (13 transformations) were coded, mainly from the posterior pulmonary (or tracheal) segment, and other 7 non-respiratory characters here added. The new data were combined with those of a previously published analysis, resulting in a data matrix of 82 characters scored for 44 terminals. The evolution of the tracheal system is traced through the phylogeny of basal spiders and the Haplogynae, and new synapomorphies are provided. Elongate 3rd abdominal entapophyses are a synapomorphy of Araneomorphae. True median tracheae are a synapomorphy of Entelegynae (convergently with Austrochilinae), as is the extreme posterior displacement and narrowing of the tracheal spiracle. Tetrablemmidae, Pholcidae, Diguetidae and Plectreuridae are united by the absence of tracheae; and these taxa are united with Scytodidae, Sicariidae and Drymusidae by the fusion of 3rd entapophyses.

Keywords: Tracheae, cladistics, abdominal muscles

Since the seminal and detailed works of Bertkau (1872, 1878), much attention has been devoted to the respiratory system of spiders. Although the morphology and diversity of respiratory structures was repeatedly used in classifications (e.g., Bertkau 1878; Petrunkévitch 1933; Forster 1970), most attempts to depict the evolution of the respiratory organs in spiders were discouraging because of incongruity with other character systems, which led some authors even to negate the value of the respiratory organs to define higher groups (Lamy 1902; Levi 1967). The efforts were unable to overcome the obstacle of evaluating all character systems simultaneously. Fortunately, cladistic theory has provided the tools to manage all data globally; and the difficult task was recently achieved for basal araneomorphs and haplogyne spiders (Platnick et al. 1991). The aim of this contribution is to investigate once again the evolutionary transformations of the respiratory system through spider phylogeny, testing previous hypotheses of relationships in the light of new data.

Homology and ontogeny of respiratory structures.—Purcell (1909) convincingly

demonstrated that lateral tracheae of araneomorph spiders originate as modifications of the posterior book lungs, and median tracheae as modifications of the entapophyses of the same segment. Median tracheae are distinguished from hollowed entapophyses (also called apodemal lobes) by their much more elongate shape, and by their thin cuticle; in some cases they still retain their connection with abdominal muscles (Lamy 1902). There has been some confusion in the literature about the “transverse duct” or “interpulmonary” or “inter-tracheal canal of communication.” In many spiders, the minute projections lining respiratory cuticles (called “spicules”) also extend to cover the innermost part of the interpulmonary or inter-tracheal furrow. For the tracheal segment, Purcell (1909: 65) called this “intertracheal canal of communication,” defined as “a canal connecting the median trunks with one another and with the lateral trunks at their base,” and identified the structure as serially homologous with the interpulmonary canal of communication. Other authors (e.g., Forster & Platnick 1984) called the same structure “transverse duct.” If not to-

pologically definite as a "duct" (as discussed by Hormiga 1994), this canal becomes a functional duct because the spicules prevent the smooth anterior and posterior walls of the furrow or tracheal vestibule from collapsing together (Purcell 1909: fig. 26). I will follow here the original and accurate wording of Purcell.

METHODS

Tracheae and other cuticular structures were observed after digestion of tissues with a 10–20% KOH solution at approximately 100 °C in a double boiler or hot plate. Dissections for muscle observations were made on regular alcohol-fixed specimens. Small structures were mounted in lactic acid or clove oil, and observed with a compound microscope. This analysis complements Platnick et al. (1991), and so numbers for characters follow that paper.

RESPIRATORY SYSTEMS OF THE REPRESENTATIVE TAXA

Most data on tracheae, entapophyses and muscle attachments were extracted from the general works by Lamy (1902), Purcell (1909, 1910), Kästner (1929), and references therein. Data on particular groups were found in Forster et al. (1987: Austrochiloidea, Hypochiloidea), Ramírez & Grismado (1997: Filistidae), Forster (1995: Scytodidae, Drymusidae, Sicariidae and Periegopidae), Platnick (1989: Diguettidae), Forster & Platnick (1985: Dysderoidea), Forster & Platnick (1984: Palpimanoidea), Platnick et al. (1999: Palpimaniidae), and Forster (1970: Entelegynae). The new data are discussed below.

Austrochilinae: There is a wide furrow linking three paired structures (Fig. 4), described by Forster et al. (1987): "the inner pair are in fact apodemes [...]. The middle pair of tubes (those immediately lateral to the apodemal lobes) could be homologous with one of the book lung lamellae, but the outer pair are more likely to represent the marginal extensions of the original atrial pouch, which in most spiders [...] tend to be arcuate." Their interpretation agrees with my observations. The inner pair connects with the median longitudinal muscles. In the early instars of *Thaida peculiaris* Karsch 1880 the intermediate pair arises during ontogeny as a flat outgrowth of the more lateral pair (Fig. 3). All

these structures are lined with spicules, including an inter-tracheal canal. In subsequent stages the modified entapophyses are indistinguishable from the true median tracheae found in Entelegynae.

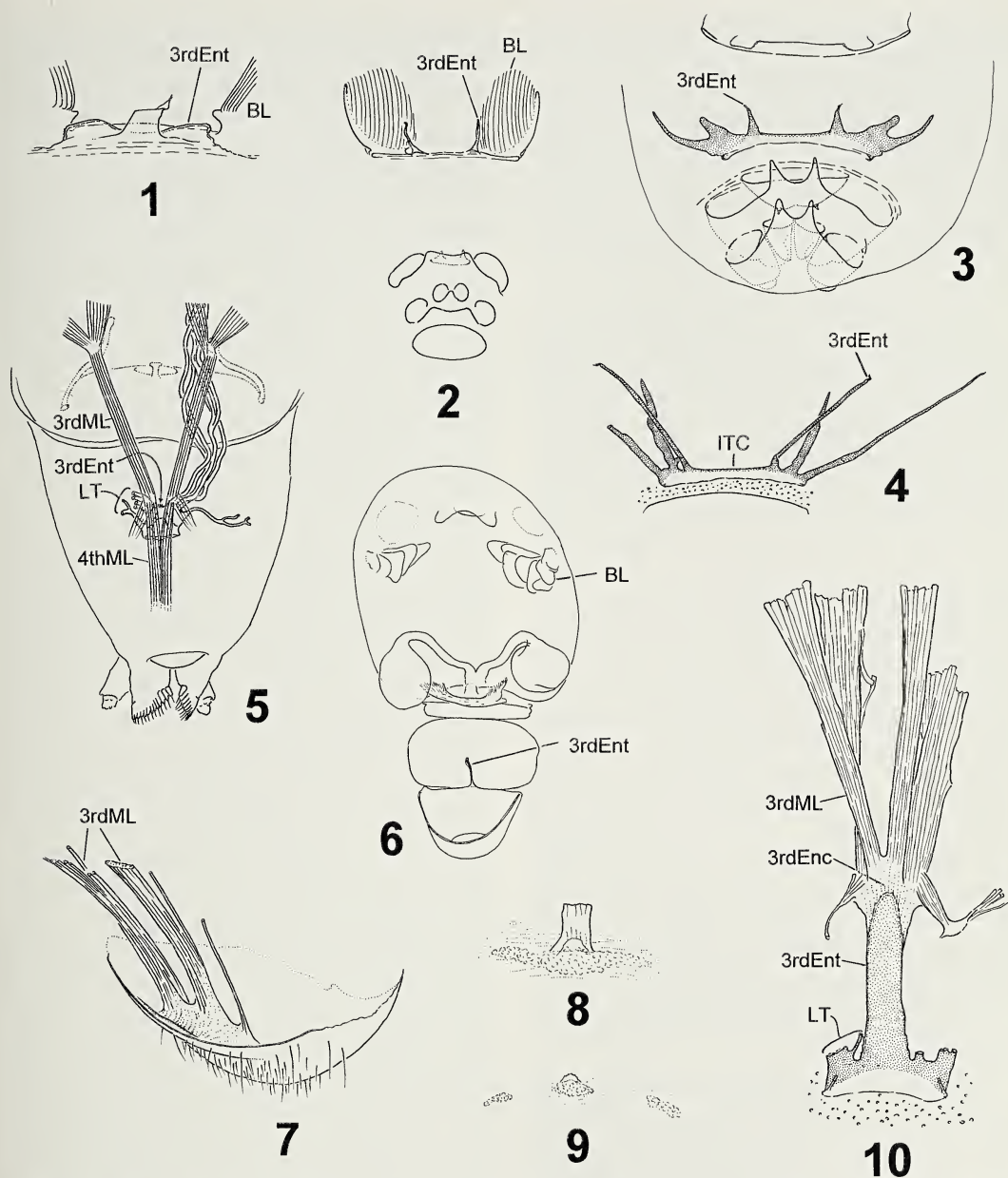
Sicariidae: In *Loxosceles laeta* (Nicolet 1849) and *Sicarius* Walckenaer 1847 spp. (from Argentina), there is a median structure homologous with the two fused entapophyses, similar to that found in *Drymusa* Simon 1891 and *Scytodes* Latreille 1804, but more elongate and thick. I found in both sicariids the expected attachment of the median longitudinal muscles that converge on the fused entapophyses (Fig. 10).

Tetrablemmidae: Platnick et al. (1991) coded the respiratory characters of *Caraimatta* Lehtinen 1981 according to the description of *Brignoliella* Shear 1978 given by Forster & Platnick (1985). It seems that they confused the ducts of the female genitalia, or the paired pits of the preanal plate, with tracheae or spiracles. In *Brignoliella* cf. *carmen* Lehtinen 1981 (from New Caledonia), and in *Caraimatta* cf. *cambridgei* (Bryant 1940), the only remnant of tracheal system is a median apodeme (Fig. 6), in agreement with Shear (1978). I also found a similar apodeme in an unidentified Pacullinae from Borneo.

Diguettidae and *Plectreuridae*: A transverse external mark indicates the place where longitudinal muscles attach, on a wide line of the abdominal cuticle (Fig. 7). The entapophyses appear to have lost, in some degree, their function of main site of muscle attachment. In *Kibramoa* Chamberlin 1924 (Fig. 8) and *Plectreurys* Simon 1893 (Fig. 9) the entapophyses are still recognizable as a short median lobe. In *Diguettia catamarquensis* (Mello-Leitão 1941) and *Segestrioides tofo* Platnick 1998 the marks on the cuticle are similar to those of Fig. 9, but the median lobe is almost unrecognizable.

Telemididae: My dissections of *Usofila* sp. (from California) showed a tracheal pattern like that of *Telema* Simon 1882, as described by Fage (1913).

Ochyroceratidae: *Ochyrocera* Simon 1891 sp. has two groups of 4–5 tubes each arising from each anterior corner of a characteristic trapezoidal vestibule (Fage 1912: fig. 73), one of them posteriorly directed. In the space between these groups, I found a pair of short



Figures 1-10.—Posterior respiratory system and abdominal structures. 1. *Liphistius sumatranus* Thorell 1890, exuvia of female, detail of 3rd abdominal entapophyses on posterior interpulmonary furrow; 2. *Hyphochilus cf. gertschi* Hoffman 1963, female from Virginia, Giles County, posterior respiratory system and spinneret's bases; 3. *Thaيدا peculiaris*, first free instar, posterior respiratory system and spinneret's bases; 4. *Thaيدا peculiaris*, subadult male, detail of posterior respiratory system; 5. *Ochyrocera* sp., female from Minas Gerais, dissected and cleared abdomen, showing median longitudinal muscles and tracheal system; 6. *Caramatta cf. cambridgei*, female from Costa Rica, digested abdomen, dorsal view; 7. *Diguetia catamarquensis*, female, dissected abdomen, anterior-lateral view, showing insertion of median longitudinal muscles; 8. *Kibramoa* sp., female from California, 3rd entapophysis and muscle insertion area; 9. *Plectreurus* sp., female from Costa Rica, muscle insertion area; 10. *Loxosceles laeta*, posterior respiratory system showing muscle insertions (lateral tracheae broken). *Abbreviations:* 3rdEnc = entochondrite at hind end of third median longitudinal muscle; 3rdEnt = third entapophysis; 3rdML = third median longitudinal abdominal muscle; 4thML = fourth median longitudinal abdominal muscle; BL = book lung; ITC = inter-tracheal canal; LT = lateral tracheae.

entapophyses, where the longitudinal muscles connect (Fig. 5).

Archaeidae: The reduced tracheal system of *Archaea workmani* (O. P.-Cambridge 1881) consists of two separate spiracles each leading to a slender median tracheae, without a transverse furrow (Forster & Platnick 1984). I found the apex of these structures widened and fibrose, typical of muscle insertions.

CLADISTIC ANALYSIS

The present data matrix includes the 43 terminals from Platnick et al. (1991), plus *Pikelinia roigi* Ramírez & Grismado 1997 (Filistatidae, Prithinae) and a root vector, all scored for 80 characters. The first 67 characters are those used in that paper; only modifications and additional characters are listed below. The root vector specifies the states plesiomorphic for Mygalomorphae and Liphistiomorphae. Polymorphisms were used to express variability in the taxa represented by the selected exemplars, and internal steps were added to account for the homoplasy while computing weights. If a representative species does not have a condition known to occur in the family it represents, I followed a strategy similar to that of Platnick et al. (1991), but coding polymorphic entries. Polymorphisms were assigned according to notes in Platnick et al. to characters 23 (in *Oecobius* Lucas 1846), 36 (in *Dysdera* Latreille 1804 and *Otiotrops* Macleay 1839), and 65 (in *Pholcus* Walckenaer 1805), and checked to ensure none required illogical optimizations. Except as noted, all characters were treated as unordered.

Character 1: Cribellum: present (0); absent (1). *Gradungula* Forster 1955 and *Pianoa* Forster 1987 are coded as 1, although the primitive state for the gradungulids should be 0. This coding does not produce an illogical optimization, as the lost cribellum appears as synapomorphy of both genera. *Character 16*: Posterior book lungs or modifications: pair of normal book lungs (0); pair of book lungs reduced to two lamellae (1); pair of lateral tracheae (2); absent (3). Filistatines are coded [012] because the homology of their short, flattened lateral structures are unclear (Purcell 1910: 558; Forster et al. 1987: 93). *Character 18*: Opening(s) of posterior respiratory system, or position of 3rd abdominal entapophyses: about midway between anterior book

lungs and spinnerets (0); just behind openings of anterior respiratory system (1); just anterior to spinnerets (2). The root is coded as [02] because the openings of posterior book lungs are just anterior to the spinnerets in Liphistiomorphae, but separated from them in Mygalomorphae. *Character 20*: Cheliceral gland mound: absent (0); present (1). The putative parallelism in *Crassanapis* Platnick & Forster 1989 was coded as 1 (Platnick & Forster 1989: fig. 11). *Character 32*: Posterior spiracles or origin of 3rd abdominal entapophyses: separate (0); contiguous (1); fused (2). This character expresses the degree of fusion of the formerly bilateral posterior respiratory organs, and is, accordingly, coded as ordered. The position of apodemes serves to discriminate between states in those cases where there is a median transverse furrow, but two interpretations (a wide median spiracle, or two spiracles linked by a furrow) are possible. *Diguetia* Simon 1895 and *Segestrioides* Keyserling 1883 are coded as uncertain because they lack definite cuticular apodemes, and the longitudinal muscles insert on a wide line. *Appaleptoneta* Platnick 1986 is also coded as uncertain because its respiratory system is unknown, and *Leptoneta* Simon 1872 has no evidence of apodemes (Lamy 1902: fig. 16). *Otiotrops* is coded [12] because of the variability found in Otiotropinae (Platnick et al. 1999). *Character 45*: Cribellum: entire (0); divided (1). *Gradungula* and *Pianoa* Forster 1987 are coded as inapplicable, with the same provisions as in character 1. Gray (1995) noted the curious optimization of the entire cribellum as primitive, given that it is homologous with paired anterior median spinnerets. Interestingly, first free instars of *Thaïda peculiaris* show a bilobate cribellum, with only one spigot on each side (Fig. 3). *Character 67*: 3rd abdominal entapophyses: short, flat or absent (0); elongate (Fig. 2) (1). I added one internal step to the character because other pholcids lack the entapophyses (Lamy 1902). *Character 68*: Shape of fused 3rd abdominal entapophyses: short, slender (0) (Lamy 1902: fig. 14); elongate, broad (1) (Fig. 10). *Character 69*: Median tracheae: absent (0); present (1). *Character 70*: Transverse furrow between posterior spiracles: present (0); absent (1). The furrow is present in arachnid outgroups and Liphistiomorphae (Fig. 1), but absent in all Mygalomorphae (e.g., Purcell 1910: 525; Forster et

al. 1987: 93). It is coded as present in those groups with a single median spiracle whenever it is still possible to discern a furrow not lined with spicules. Some authors that overlooked that furrow interpreted the structures as two separate spiracles (e.g., Millidge 1986; revised by Hormiga 1994). *Character 71*: Inter-tracheal canal: absent (0); present (1). Scored as uncertain in those terminals without spicules through the tracheal system. *Mallecolobus* Forster & Platnick 1985 is coded [01], as the canal is present in *Orsolobus* Simon 1893 and *Falklandia* Forster & Platnick 1985, but absent in *Mallecolobus* and other orsolobids (Forster & Platnick 1985: 225). The same is true for *Segestria* Latreille 1804, as the canal is present in *Ariadna* Audouin 1826 (op. cit.). *Character 72*: Dysderoid lateral tracheae: absent (0); present (1). Each tracheal spiracle connects with a broad trunk anteriorly directed. At its base arises a small trunk that provides tracheoles to the posterior part of the abdomen. Also present in caponiids (Purcell 1910). *Character 73*: Bunch of prosomal tracheoles on lateral tracheae: absent (0); present (1). Typical of dysderoids and Caponiidae. *Character 74*: Anterior book lungs: present (0); transformed into tracheae (1). *Ochyrocera* is coded as [01], as *Theotima* sp. (from Argentina) have tracheae (pers. obs.), but at least some *Ochyrocera* have lung leaves still recognizable. *Character 75*: 3rd dorso-ventral abdominal muscles: present (0); absent (1). Although present in Liphistiomorphae and related arachnids, it is coded as [01] for the root, because some Mygalomorphae (at least) seem to lack these muscles (*Acanthogonatus centralis* Goloboff 1995, and unidentified Theraphosidae, pers. obs.). Abdominal musculature was studied in only a few taxa. The muscles were not found in normal dissections of *Gradungula sorenseni* Forster 1955, *Scytodes* sp. (from Buenos Aires), *Diguetia catarquensis*, *Mecysmauchenius segmentatus* Simon 1884 and *Otiotrops birabeni* Mello-Leitão 1945, but these observations must be considered preliminary until more refined techniques are employed. Filistatids were coded according to Ramírez & Grismado (1997). All other codings are from Millot (1936). *Character 76*: Leg autospasy: between coxa and trochanter (0); between patella and tibia (1). *Hypochilus* Mark 1888 is coded as uncertain, because it lacks definite regions for

leg autospasy (Petrunkévitch 1933: 347). *Character 77*: Excavation between male palpal femur and trochanter, into which the embolus fits (Ramírez & Grismado 1997): absent (0); present (1). *Character 78*: Three synapomorphies for Filistatidae (Gray 1995; Ramírez & Grismado 1997): absent (0); present (1). *Character 79*: Supra-anal organ: absent (0); present (1). A synapomorphy of Diguetiidae (Lopez 1983; Platnick 1989). *Character 80*: Bipectinate claws: absent (0); present (1). Coded as [01] in *Dysdera* because the single row of teeth in dysderids seems to retain traces of two rows (Forster & Platnick 1985: 218). *Character 81*: Proprioceptor bristles on tarsi: absent (0); present (1). A synapomorphy of orsolobids plus at least some oonopids (Forster & Platnick 1985: 219, 227; Platnick et al. 1991: 67).

The data matrix of Table 1 was analyzed under parsimony using implied weights (Goloboff 1993, 1995), using Pee-Wee version 3.0 (Goloboff 1999). This program assigns lower weight to characters with more homoplasy. Internal steps of characters were assigned as implied by polymorphic terminals with command *cocode=*. The same tree of Fig. 11 is found for any value of the constant of concavity *K* ($1 \leq K \leq 6$). Under *K* = 3, 80% of the independent replications of Wagner trees followed by TBR branch swapping (command *mult*N*;) produces the same optimal tree, thus it is likely an exact solution. The tree is 243 steps long, which is two steps longer than the 20 trees obtained under equal weights with Nona (Goloboff 1999). In these trees, steps are saved in some homoplasious characters (like the anterior median eye loss, and the inter-tracheal canal) at expenses of less homoplasious ones (independent acquisition of retrolateral tibial apophysis, and reversion to a primitive tapetum).

DISCUSSION

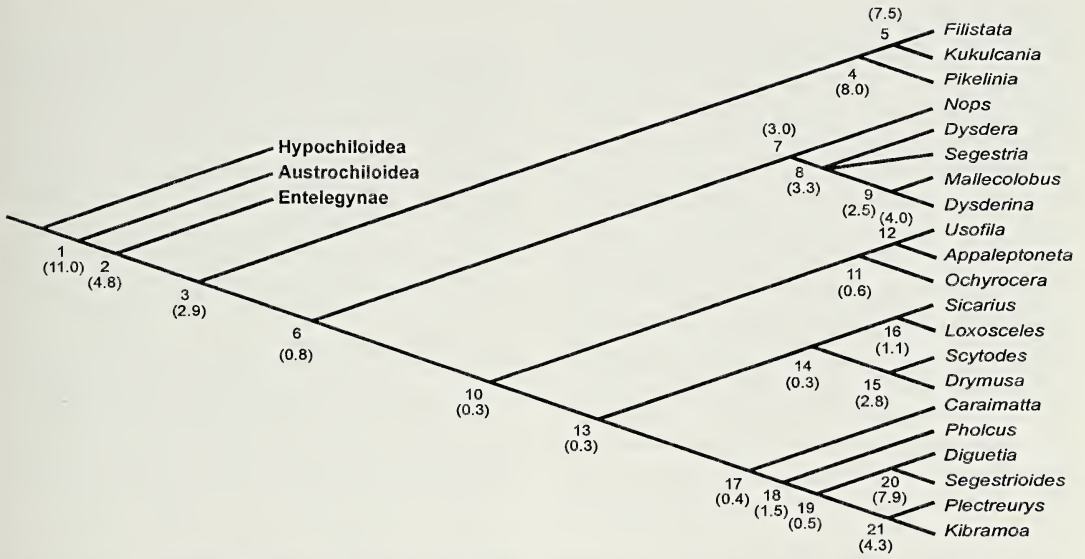
Forster (1995) discussed the phylogeny of haplogyne spiders proposed by Platnick et al. (1991) in the light of additional characters from the tracheal system. He proposed the group Sicarioidea coincident with Simon's (1893) Sicariidae, composed by Sicariidae, Scytodidae, Periegopidae, Drymusidae, Plectreuridae, and Diguetiidae, all united by the fusion of the third entapophyses. The present analysis that takes into account all characters

Table 1.—Modifications and additional characters for the data matrix of Platnick et al. (1991). *Pikelinia* scores as *Kukulcania* for all characters not shown here. v = [01], w = [012], x = [12], y = [02], ? = unknown, — = inapplicable. Prior weight applied as: character 27 (weight 10), 28(14), 28(2), 51(5), 76(3). Internal steps implied by polymorphisms as: character 23, 32, 33, 39, 65, 67, 74, 80 (1 step); 36, (2 steps); 70 (4 steps); 71 (3 steps).

Character	16	18	32	67	70	75	80
root	0	y	0	000	00000	v0000	00-
<i>Hypochilus</i>	0	0	0	1-0	00000	0-000	000
<i>Ectatostisca</i>	0	0	0	1-0	0?000	10000	00?
<i>Gradungula</i>	0	0	0	1-0	00000	10000	00-
<i>Pianoa</i>	0	0	0	1-0	0?000	?0000	00-
<i>Hickmania</i>	0	0	0	1-0	0?000	?0000	00?
<i>Austrochilus</i>	1	0	0	1-1	01000	?1000	001
<i>Thaïda</i>	1	0	0	1-1	01000	?1000	001
<i>Pikelinia</i>	3	0	0	1-0	1-000	01100	00?
<i>Filistata</i>	w	0	0	1-0	01000	01110	000
<i>Kukulcania</i>	w	0	0	1-0	01000	01110	000
<i>Scytodes</i>	2	0	2	100	01000	10000	10-
<i>Sicarius</i>	3	0	2	110	--000	10000	00-
<i>Drymusa</i>	2	0	2	100	01000	?0000	00-
<i>Loxosceles</i>	2	0	2	110	01000	10000	00-
<i>Diguetia</i>	3	0	?	000	--000	10001	00-
<i>Segestrioides</i>	3	0	?	000	--000	?0001	00-
<i>Plectreurys</i>	3	0	2	000	--000	?0000	00-
<i>Kibramoa</i>	3	0	2	000	--000	?0000	00-
<i>Pholcus</i>	3	0	1	000	--000	10100	00-
<i>Caraimatta</i>	3	0	2	100	--000	?0000	00-
<i>Nops</i>	2	1	0	000	01111	?0000	00-
<i>Ochyrocera</i>	2	0	1	000	0-00v	?0000	00-
<i>Segestia</i>	2	1	0	000	vv110	10000	00-
<i>Dysdera</i>	2	1	0	000	10110	10000	v0-
<i>Mallecolobus</i>	2	1	0	000	vv110	?0000	11-
<i>Dysderina</i>	2	1	0	000	01110	?0000	11-
<i>Appaleptoneta</i>	2	0	?	?-?	0?000	?1000	00-
<i>Usofila</i>	2	0	0	?-?	10000	?0000	00-
<i>Archaea</i>	3	0	0	1-1	10000	?0000	00-
<i>Mecysmauchenius</i>	2	0	1	1-1	01000	10000	00-
<i>Tricellina</i>	2	2	1	1-1	01001	?0000	00-
<i>Huttonia</i>	2	0	2	111	01000	?0000	00-
<i>Othiotops</i>	2	0	x	000	01000	10000	00-
<i>Waitkera</i>	2	0	1	1-1	01000	00000	001
<i>Tetragnatha</i>	2	2	1	1-1	01000	10000	00-
<i>Crassanapis</i>	2	2	1	1-1	01000	?0000	00-
<i>Oecobius</i>	2	2	1	1-1	01000	00000	001
<i>Stegodyphus</i>	2	2	1	1-1	01000	00000	001
<i>Deinopis</i>	2	2	1	1-1	01000	?0000	001
<i>Dictyna</i>	2	0	1	1-1	01000	00000	001
<i>Callobius</i>	2	2	1	1-1	01000	?0000	001
<i>Araneus</i>	2	2	1	1-1	01000	00000	00-
<i>Mimetus</i>	2	2	1	1-1	01000	?0000	00-
<i>Pararchaea</i>	2	2	1	1-1	01000	?0000	00-

from both sources (but revises some observations), yields intermediate results. In agreement with Forster's hypothesis, my analysis retrieves a monophyletic group with fused en-

tapophyses, but including Tetrablemmidae, after the re-examination of their tracheal system. However, the placement of Pholcidae coincides with that of Platnick et al. 1991. It must



Figures 11.—Optimal cladogram for the representative taxa. Bremer support in terms of Fit are given on each node.

be noticed that the differences between my results and those of Platnick et al. involve groups with relatively low Bremer support (Bremer 1994; values on Fig. 11), which might be the most prone to change should new characters (e.g., from female genitalia) or representatives (e.g., from Pacullinae and Theotiminae) be added.

The elongate entapophyses (char. 67) are a synapomorphy of Araneomorphae, with a subsequent reversion in the Haplogynae other than filistatids (node 6), and regain in Scytodidae, Sicariidae and Tetrablemmidae as a central, fused element (see below). Confirming the hypothesis of Purcell (1909), the short apodemes of Segestriidae (and their relatives) are reduced entapophyses rather than reduced median tracheae. As supposed by the same author, the loss of the transverse furrow (char. 70) is a synapomorphy of the suborder Mygalomorphae, with parallelisms in some isolated araneomorph groups. Although homoplasy seems to be rampant in this character, no parallel gains of a transverse furrow have been mapped. The inter-tracheal canal appears in Araneoclada or Neocribellatae (ambiguous optimization), and is independently lost in several araneocladan clades. Lateral tracheae (char. 16 -state 2) are a synapomorphy of Araneoclada (node 2), whereas the reduction of posterior book lungs to two pulmonary leaves

(char. 16-1) is a synapomorphy of Austrochilinae.

Within the Haplogynae, filistatines (node 5) were repeatedly described as having some relict of book lungs instead of lateral tracheae. Because the optimization of the character gives state 2 at the base of Filistatinae, the congruence criterion suggests that these structures are homologous with lateral tracheae. The 3rd dorsoventral abdominal muscles (char. 75) have been lost several times in this tree, but were never found in haplogynes other than Filistatidae. The loss of lateral tracheae (char. 16-3) is a synapomorphy of node 17, with parallelism at least in Prithinae (*Pikelinia* Mello-Leotão), *Sicarius*, and dictynids. The advanced spiracles (char. 18-1) are a synapomorphy of caponiids (*Nops* MacLeay 1838) and Dysderoidea (node 8), but the placement of Tetrablemmidae (*Caraimatta*) is different from that of Platnick et al. because of the re-examination of the tracheal system of tetrablemmids. The fused entapophyses (char. 32-2) are a synapomorphy of node 13 plus Periegopidae; this last group was not included here but seems to be the undisputed sister group of Scytodidae (Forster 1995). For this data matrix there is a reversion to state 1 in *Pholcus*, but conditions in other pholcids range from a pair of contiguous entapophyses linked by a furrow, to the smooth concave cu-

ticle serving directly as the site for muscle attachment. Further elongation of the fused entapophyses is a synapomorphy of Sicariidae. All book lung reductions (char. 74) have independent origin for this data set.

Three characters of the respiratory system are synapomorphies of Entelegynae: The first is the extreme posterior displacement of the spiracle (char. 18-2), with homoplasy in several palpimanoids, dictynids, Uloboridae, and many derivative groups not included in the analysis. The second is the contiguous median tracheae (homologous with 3rd entapophyses, char. 32-1), although the same state appears to arise convergently (but without true median tracheae) in *Ochyrocera* and *Pholcus*. The third is true median tracheae (char. 69), with a notable convergence in Austrochilinae.

A scenario of the morphological transformations leading to the median tracheae can be traced by optimizing characters on the phylogeny. Basal spiders (and closer outgroups) have hollowed thick entapophyses, arising from an interpulmonary furrow. The entapophyses elongated in Araneomorphae. The spicules typical of respiratory cuticles extended from posterior book lungs (in an ancestor of the Neocribellatae) or from lateral tracheae (in an ancestor of Araneoclada) to line the furrow, forming an inter-tracheal canal. At the same time, or later in some ancestor of the Entelegynae, the spicules lined also the interior surface of entapophyses, that became elongated and slender, with thin cuticle, forming the median tracheae. This transformations series was hypothesized by Purcell as early as 1909.

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EFFECTS OF CLIMATE AND PREY AVAILABILITY ON FORAGING IN A SOCIAL SPIDER, *STEGODYPHUS MIMOSARUM* (ARANEAE, ERESIDAE)

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ABSTRACT. Tropical areas with favorable climatic conditions, high prey availability and large prey size are assumed to favor sociality in spiders. Notwithstanding, the three social species of *Stegodyphus* (Eresidae) inhabit arid and semi-arid habitats with marked daily and seasonal variation in climate. The nests of the social spider *Stegodyphus mimosarum* Pavesi commonly occur in dry Acacia savanna in southern Africa. We investigated the abiotic conditions to which the nests of *S. mimosarum* are exposed and the changes in availability of potential insect prey at different times of year and over the daily cycle. We used these data to determine the extent to which prey availability and climatic conditions explain seasonal and daily variation in the activity of the spiders. Data were collected during four sampling periods a year over two years from nests of *S. mimosarum* located on the Mkomazi River Bridge (KwaZulu-Natal, South Africa). We measured ambient and nest temperatures and in a sample of nests, spider growth rate, prey availability, foraging activity and activity on the web at night. Spiders had two periods of increased growth rate occurring in early and late summer, at times of year when ambient temperature rarely falls below 20 °C. Temperatures inside the nest were generally higher than ambient throughout the day and night. Foraging response, measured as the numbers of individuals responding to the vibrations of a tuning fork, was significantly higher by night than by day. In summer, foraging response decreased with increasing temperature during the day, whereas in winter, there was a positive correlation between foraging response and temperature at night. Potential prey, measured as mean numbers of insects trapped in a sample of webs, were more abundant during the day than at night, despite the fact that the spiders were most active on the web at night. Nocturnal insects, however, were larger than diurnal ones and spiders handled significantly more large prey both during the day and at night. Correlation and partial correlation analyses indicate that ambient temperature and windspeed play a direct role in influencing foraging and other activity on the web. Nonetheless, the predominance of nocturnal activity in both summer and winter could not be explained by climatic conditions and prey availability alone. Some other factor (e.g., predation or parasitism) may be involved.

Keywords: Climate, prey availability, foraging, social spider

Most of the 18 or so known species of social spiders (also referred to as cooperatively group-living or permanently social) are tropical, and most are found in the wet tropics (D'Andrea 1987; Avilés 1997). Sociality may occur with greater frequency in the tropics because the benign climate allows activity to be maintained year-round, and thus a colony can be maintained continuously over several generations, or because potential insect prey are available year-round, also allowing continuous activity (Riechert 1995). Additionally, large insects, which can be captured more ef-

ficiently by a group of spiders than by solitary spiders of a similar size (Nentwig 1985), are more abundant in the tropics (Rypstra 1990).

Notwithstanding, the three social species of *Stegodyphus* (Eresidae) (and indeed, most of the remaining 17 solitary species of the genus) are sub-tropical and live in arid, semi-arid and seasonally wet savannas of Africa and the Indian subcontinent (Kraus & Kraus 1988). The two African species, *S. dumicola* and *S. mimosarum*, occur largely in dry thornbush (Acacia) savanna, where summer temperatures are high and winter is generally cold,

with little plant growth or insect activity. *Stegodyphus* colonies have a strongly seasonal developmental cycle, which is linked to the local seasonal regime (Seibt & Wickler 1988). Consequently, we expect to find a strong correlation between variation in the physical and biotic environment and both daily and seasonal activity of spiders in *Stegodyphus* colonies. We investigated the abiotic conditions to which the nests of *S. mimosarum* are exposed at different times of year and the changes in availability of potential insect prey. We used these data to examine the hypothesis that prey availability and abiotic conditions explain seasonal and daily variation in the activity of these spiders.

METHODS

Natural history and study area.—Nests of *S. mimosarum* often occur near water, in the canopy of thorny acacia and other trees, as well as on man-made structures such as utility poles, road signs, fences and bridges (Kraus & Kraus 1988; Seibt & Wickler 1988; pers. obs.). Our study population consisted of nests that occupied the railing of the Mkomazi River bridge, 23 km west of Richmond in KwaZulu-Natal (29°54'31"S, 30°05'35"E). The bridge spans 66 m and is 8 m wide. The 354 vertical aluminum struts on each side of the bridge support a horizontal handrail at a height 1 m above the ground. The nests occupy the underside of the railing between the vertical struts along both sides of the bridge. At the start of the study in January 1995, there were 615 nests on both sides of the bridge combined. At this time these nests were at most nine years old, as the 1987 floods destroyed the railings together with any nests. Nests occurred also in the canopies of trees downstream from this site and on trees growing on pylons below the bridge. These latter nests were difficult to access.

The annual rainfall for the area for 1994 was 630 mm, 1041 mm for 1995 and 1112 mm for 1996. Most rain fell in summer (October–February). Summer temperatures regularly exceeded 35 °C and during winter dropped below 0 °C.

Data collection.—The study was conducted from January 1995 to November 1996. We measured body size (length from the tip of the prosoma to the tip of the abdomen) of individuals from 20–30 randomly selected nests

at different times of year. Measurements of abiotic and biotic factors were conducted over a 3-day period, once every 4 months (February, May, August, November). Forty to sixty nests were randomly selected for each observation period (20–30 nests from each side of the bridge). We measured nest, web and ambient temperatures, windspeed, spider activity and prey availability. Diurnal data were collected over three days during each month sampled in 1995. Nocturnal data were collected during two nights each in May and August 1996, and from a single night each during November and February (1996). Time of day is local time (GMT +2 hours).

Nest conditions: Temperatures were measured from a single nest on the south side of the bridge. Measurements were taken inside the nest, about 2 cm below the surface and 3 cm below the nest in the capture web on the north and south sides. These measurements were taken using copper-constantan thermocouples. A temperature probe and anemometer were placed at nest height to measure ambient temperature and windspeed respectively. Temperatures and windspeeds were recorded at three five-minute intervals every hour by an MCS120-02 datalogger (M C Systems, Steenberg, Cape Town, South Africa) and hourly means were then calculated and summarized separately for day and night periods.

Prey availability: Nests were surveyed at two-hour intervals for new prey items that were either trapped on the web or were being handled by the spiders. The numbers of spiders handling the prey, prey size (mm) and identity to order level were noted.

Foraging response: Foraging response was assessed as the number of spiders responding to the vibrations emitted from a musical tuning fork (440 Hz) which are similar to vibrations produced by buzzing insects trapped in the web (Henschel et al. 1992). The stimulus was applied to the capture web 4 cm below the nest. The number of spiders emerging from the nest or approaching the vibrating tuning fork within 5 seconds was counted at two-hour intervals throughout the observation period. This behavior provided a relative measure of the readiness of spiders to attack prey caught in the web and allowed us to compare the spider's response to a standardized stimulus under different ambient conditions.

Activity on the web at night: Spiders that

emerged from the nest at night were observed under red light. Activities on the nest surface and on the capture web included construction (spinning), maintenance (the removal of old prey and silk) and prey capture. In addition, some individuals were stationary on the nest surface or on the web. The number of spiders on the web and nest surface was recorded at two-hour intervals prior to measuring foraging effort with the tuning fork.

Statistical analysis.—Temperatures measured at different locations (inside the nest, on the web, ambient) were compared using paired *t*-tests (two-tailed) on the mean hourly temperatures for the three days or two nights of each sample period. Data for each month were tested separately both here and in all other comparisons. As the same null hypothesis was being tested on each of the three days sampled (e.g., nest temperature did not differ from ambient), a Bonferroni correction was used and the acceptable level of significance ($P = 0.05$) was divided by *k*, the number of non-independent tests ($k = 3$ and 2 for diurnal and nocturnal data, respectively) (Haccou & Meelis 1994). Chi-squared tests for independence were conducted for prey data where the variables included in the analysis were the type of prey (order), prey size classes and the number of spiders handling prey (Zar 1984).

Relationships between the variables (ambient temperature, windspeed, prey, foraging response and spider activity) were tested with Pearson's product-moment correlation and Spearman's rank correlation. Partial correlation analysis (Zar 1984) was used to determine the correlation between any two variables while maintaining all others constant.

Data on prey availability and foraging activity required logarithmic transformation prior to analysis and values were replaced by $\log(x + 1)$ (Elliot 1983).

RESULTS

Growth rate and seasonal development of spiders.—*Stegodyphus mimosarum* appeared as juveniles in February, were sub-adult from October to December, and reached maturity in summer from December to February when mating and egg laying took place (Fig. 1). Little growth occurred during the winter months (May to August). In 1996, individual growth during the winter months (May–July) was less than 5% per month (av-

eraging 1.7–4.3%, in body length), whereas in summer spiders grew 13.3–16.6% per month in body length.

Seasonal changes in temperature and windspeed.—*Diurnal conditions:* During February, which is late summer and the hottest month sampled, the temperature inside the nest was on average 2.5 °C higher than ambient ($t = 4.64$, $P < 0.001$) (Fig. 2). During February a maximum of 41.7 °C was recorded within the nest and 36.6 °C for ambient temperature. Temperatures below the nest, on the south and north sides of the railing, were not significantly different from ambient. However, they were on average 3.0 °C ($t = 5.65$, $P < 0.001$) and 2.8 °C ($t = 5.17$, $P < 0.0001$) respectively, lower than temperatures within the nest. At high ambient temperatures (± 30 –35 °C), spiders were observed sitting below the nest in a layer of loose silk on the nest surface, as well as just inside the nest entrances. Throughout the remainder of the year (i.e., May, August and November), temperatures measured inside the nest did not differ significantly from ambient, nor from those on the north and south side of the nest. However, temperatures within the nest were generally above those on the web. Maxima recorded for ambient and nest temperature were 33.2 °C and 37.7 °C, respectively for May, and 32.2 °C and 32.8 °C for November. Windspeed was highest during the summer months of November and February (Fig. 2).

Nocturnal conditions: During February and August nighttime temperatures within the nest were only slightly, but significantly higher than ambient (Fig. 2). Temperatures inside the nest were on average 1.0 °C higher than ambient ($t = 2.62$, $P = 0.01$) in February and 0.9 °C in August ($t = 2.50$, $P = 0.013$). In winter (May) and early summer (November) nest and ambient temperatures showed similar patterns, but they were not significantly different. Nest temperatures were at a minimum of 7.1 °C in August, when minimum ambient was 6.1 °C, and at a maximum of 27.7 °C in February, when maximum ambient reached 27 °C. Nighttime windspeed was highest in the summer months (November–February, Fig. 2).

Daily changes in temperature and windspeed.—Mean ambient and nest temperatures reach a maximum between 1200–1400 h and were at a minimum before sunrise (Fig. 3).

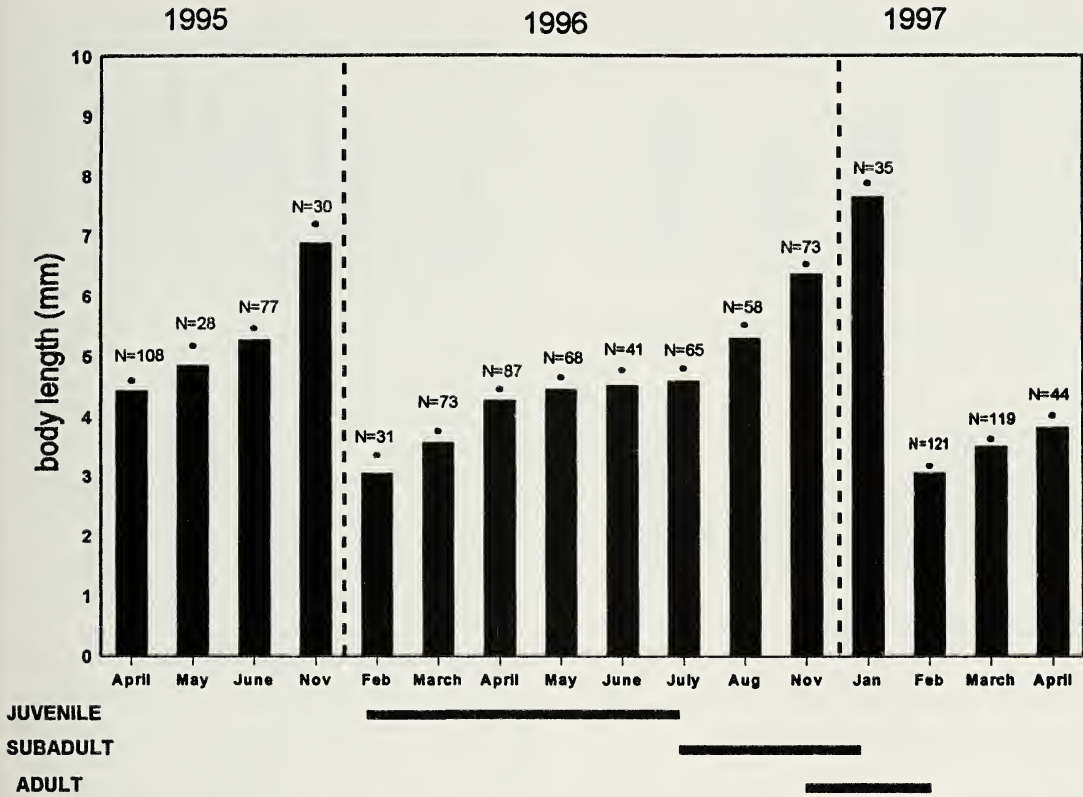


Figure 1.—Mean and 95% confidence intervals (dots above bars) for body length of *Stegodyphus mimosarum* and the period of occurrence of different life stages on the bridge.

During winter (May–August) the temperature differences between day and night were extreme, resulting in rapid loss of heat from the nest from midday to sunset, and rapid heat gain from sunrise to midday (Fig. 3). Nest and ambient temperatures in winter (August) remained well below 25 °C throughout the day. During the hottest month (February), temperatures inside the nest were above 30 °C from 1000–1400 h.

Daytime windspeeds peaked at 1600 h and were both greater and more variable than those measured at night. Wind and temperature were not significantly correlated, apart from nighttime records in February and May (Spearman rank correlation, $R = 0.465$, $P = 0.004$, $n = 36$ and $R = 0.374$, $P = 0.009$, $n = 75$, respectively).

Prey Availability.—*Prey numbers:* Throughout the year the greatest numbers of prey were found on the web between 0800–1000 h; the greatest numbers of prey per web were in the summer months (May–November;

Fig. 4). With the exception of November, very few prey items were observed in the webs during the night (1900–0500 h), despite the fact that the spiders were most active at this time (see below). In all months, more insects were trapped in *S. mimosarum* webs (= available prey) during the day than at night. A single insect was trapped at night in a survey of approximately 50 webs in each of the sampling months of February and August (late summer and late winter, respectively). In May (early winter) and November (early summer) respectively, 4% and 12% of the insects trapped were nocturnal. While these figures represent insects that landed on the web and were available to spiders, not all of these insects were actually captured by the spiders (Table 1). There was no significant difference between the numbers of insects actually handled by day and night. However, proportionally more nocturnal insects were handled (83% and 78% of trapped insects in May and November, respectively), whereas only 5–25%

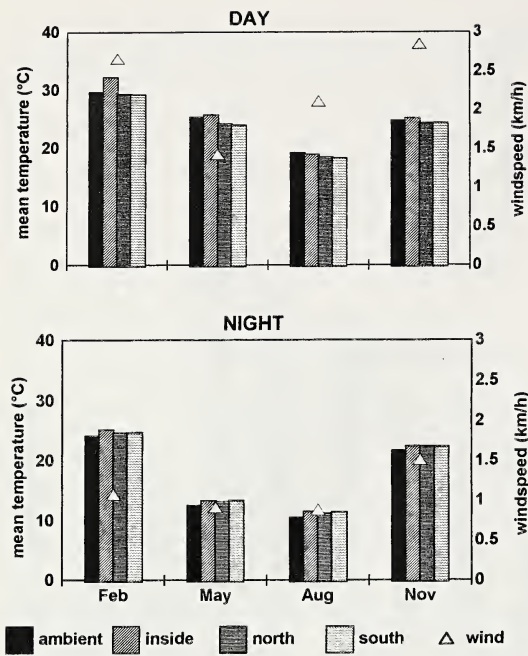


Figure 2.—Mean windspeed (km/h), ambient temperature (°C) and temperatures inside and below the nest on the north and south side.

of diurnal insects were handled by the spiders (Table 1).

We compared the sizes of insects trapped in the webs with those of prey actually handled by the spiders, and similarly, the types of insects trapped and handled. Because of small

sample sizes in some months, we pooled the data from all sampling dates for the statistical analyses.

Prey size: Most insects trapped in the capture webs were < 3 mm in body length (Table 1). Despite their availability, insects of this size class were rarely handled by the spiders. Medium sized prey (3–6 mm) and larger insects (> 6 mm) were handled significantly more often than expected from their abundance in the webs by day (all seasons combined, $\chi^2 = 164.8$, $df = 3$, $P = 0.0001$). A large proportion of the prey available at night was greater than 3 mm in length and there was no significant difference between the size of prey available and those handled at night (all seasons combined, $\chi^2 = 1.32$, $df = 2$, $P > 0.05$).

Prey type: The prey taxa available changed throughout the year. Diptera were common in all samples, Ephemeroptera were most common in February; Hemiptera and Coleoptera in May and November, and Hymenoptera in November (Table 2). There were significant differences in the distribution of major taxa available in the web and those handled by the spiders during the day (all seasons combined, $\chi^2 = 32.98$, $df = 4$, $P = 0.001$). By day, more Coleoptera and Diptera, and fewer Hemiptera, were handled than expected. Nocturnally, prey taxa available in the web and those handled by spiders did not differ statistically. Three-

Table 1.—The distribution of size classes of prey available to the spiders (insects trapped in webs) and the corresponding percentage handled by them.

Size classes	February		May		August		November	
	Day	Night	Day	Night	Day	Night	Day	Night
Prey available in webs (%)								
<1 to 3 mm	58.1	0	64	33.3	37.2	100	80.9	7.3
3.1 to 6 mm	19.3	100	12.8	50.1	37.6	0	16	21.8
6.1 to 15 mm	19.3	0	20.5	8.3	25.5	0	2.7	56.4
>15 mm	3.2	0	2.7	8.3	0	0	0.4	14.5
Total prey available	31	1	326	12	43	1	406	55
Prey handled (%)								
<1 to 3 mm	0	0	0.6	25.1	0	100	0.7	0
3.1 to 6 mm	3.2	100	2.5	41.6	2.3	0	0	14.5
6.1 to 15 mm	16.1	0	8.8	8.3	2.3	0	0.7	49.18
>15 mm	3.2	0	2.5	8.3	0	0	0	14.5
Total prey available	7	1	47	10	2	1	6	43
Prey handled as % of total prey available								
	22.5	100	14.4	83.3	4.6	100	1.4	78.2

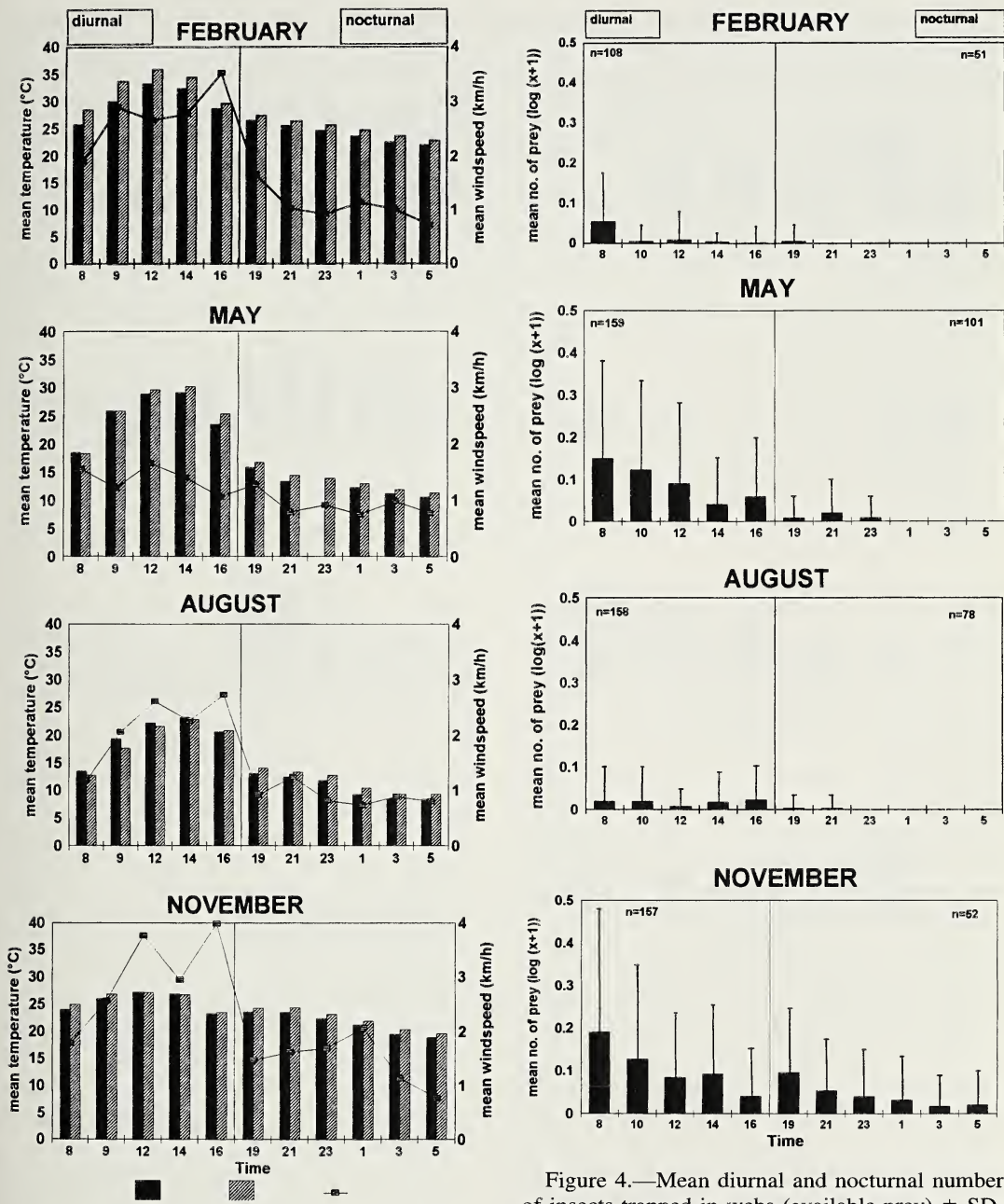


Figure 3.—Mean diurnal and nocturnal ambient temperature, nest temperature (°C) and windspeed (km/h).

Figure 4.—Mean diurnal and nocturnal numbers of insects trapped in webs (available prey) \pm SD.

way contingency tables (partial independence) tested for interactions between prey size and type for all seasons. We found for both day and night there was a lack of independence between prey size and type in influencing whether the prey was handled (day: $\chi^2 =$

197.6, $df = 8$, $P = 0.0001$; night: $\chi^2 = 15.58$, $df = 6$, $P = 0.016$).

Foraging response.—The response of spiders to a prey stimulus (tuning fork) was greater at night than during the day: February, $t = -17.3$, $P = 0.001$; August, $t = -4.2$, $P = 0.012$ and November, $t = -10.3$, $P = 0.001$ (Fig. 5). For all of these $P < 0.013$, the Bonferroni-adjusted level of alpha. Diurnal for-

Table 2.—The distribution of taxa of prey available to the spiders (insects trapped in webs) and the corresponding percentage handled by them.

Prey type	February		May		August		November	
	Day	Night	Day	Night	Day	Night	Day	Night
Prey available in webs (%)								
Coleoptera	3.2	100	16.8	16.6	0	0	3.2	47.7
Diptera	29	0	49.6	50	76.7	100	13.3	10.9
Hemiptera	22.5	0	26.9	0	4.6	0	38.4	3.6
Hymenoptera	9.6	0	3.3	25	0	0	22.1	34.5
Other	35.7	0	4.3	8.4	18.7	0	23	3.3
Total prey available	31	1	326	12	43	1	406	55
Prey handled (%)								
Coleoptera	3.2	100	2.7	8.3	0	0	0.2	38.1
Diptera	9.6	0	9.8	41.6	4.6	100	0.2	3.6
Hemiptera	0	0	1.2	0	0	0	0.4	1.8
Hymenoptera	9.6	0	0.3	25	0	0	0	32.7
Other	0	0	0.3	8.3	0	0	0	1.8
Total prey handled	7	1	47	10	2	1	6	43

aging response was higher in May than other months and spider activity was not significantly different by night and day ($t = -3.62$, $P > 0.013$). With the exception of February, foraging response decreased in the second half of the night, from about 0100 h. A similar pattern was observed when we used the proportion of nests in which spiders responded rather than mean number of spiders responding. The diurnal response levels varied considerably, with peaks occurring at different times of the day throughout the year (Fig. 5). February, May and August had higher response levels than November. This is at least in part attributable to the presence of young spiders in the nests during this period, whereas in November most spiders were subadult or adult; and the colonies contained fewer individuals owing to mortality during the growth phase.

Nocturnal activity on the web.—Shortly after sunset, spiders emerged from the nest and dispersed over the nest surface and capture web where they engaged in web cleaning, construction, or were motionless on the nest or web. The numbers emerging from the nests were highest between 0300–0400 h in February and November (summer) and between 1900–2100 h during the winter months (May and August) (Fig. 6). All spiders returned to the nest shortly before sunrise.

Relationships between activity, prey availability and abiotic factors.—Foraging

response was correlated with climatic variables and prey availability in some instances and not in others (Table 3). By day foraging was negatively related to windspeed in all four sampling periods, with the probability of $0.5^4 = 0.063$ of a negative relationship occurring by chance alone in all four samples. There was no significant correlation between foraging response and windspeed at night. Daytime foraging response was negatively correlated with ambient temperature in November (summer), while at night foraging response showed a strong positive correlation with ambient temperature in August, which was the coldest month. Prey availability and foraging response were significantly positively correlated only in February (daytime sample), however all 6 correlation coefficients were positive, with a probability of this occurring by chance alone of $0.5^6 = 0.016$.

Partial correlation analysis allowed for the comparison of two variables whilst holding constant the influence of other variables on the two in question. These results show a similar pattern to that obtained for the simple correlation (Table 3). Spider activity on the web at night was positively correlated with ambient temperature in August, as was the foraging response at night, and foraging response and activity were strongly positively correlated. During August the partial correlation coefficients for both foraging response and spider activity with ambient temperature were positive and

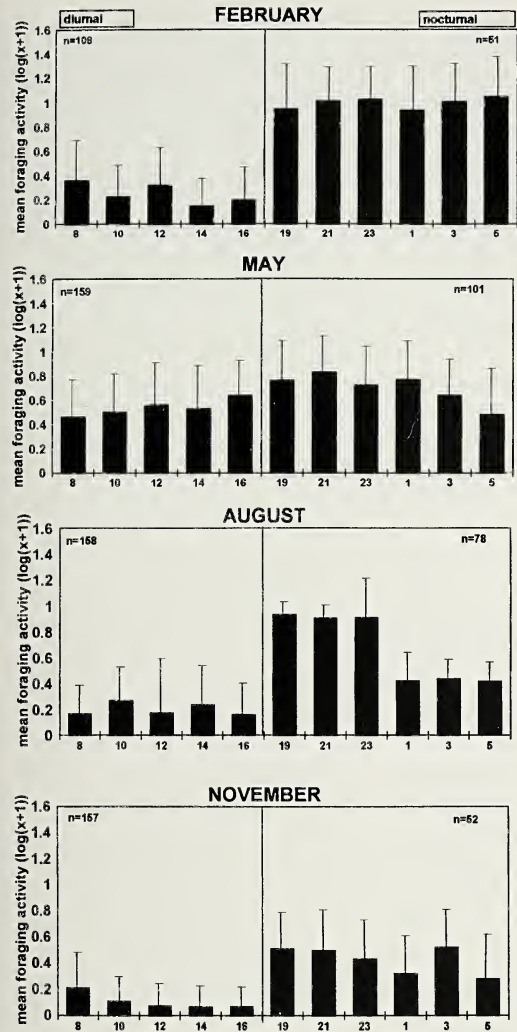


Figure 5.—Mean diurnal and nocturnal spider foraging activity (number of spiders approaching vibrating tuning fork in 5 seconds) \pm SD.

significant, suggesting that nighttime activity is strongly dependent on ambient temperature during the cool season.

DISCUSSION

Seasonality of spider growth.—The seasonality of growth and the range of spider sizes observed here was similar to those of colonies observed in other parts of KwaZulu-Natal (unpubl. data) and by Seibt & Wickler (1988). There was little spider growth in winter (May, August), when very small young were present in the nest and after the females had died. Growth to maturation and egg-laying occurred in the summer months.

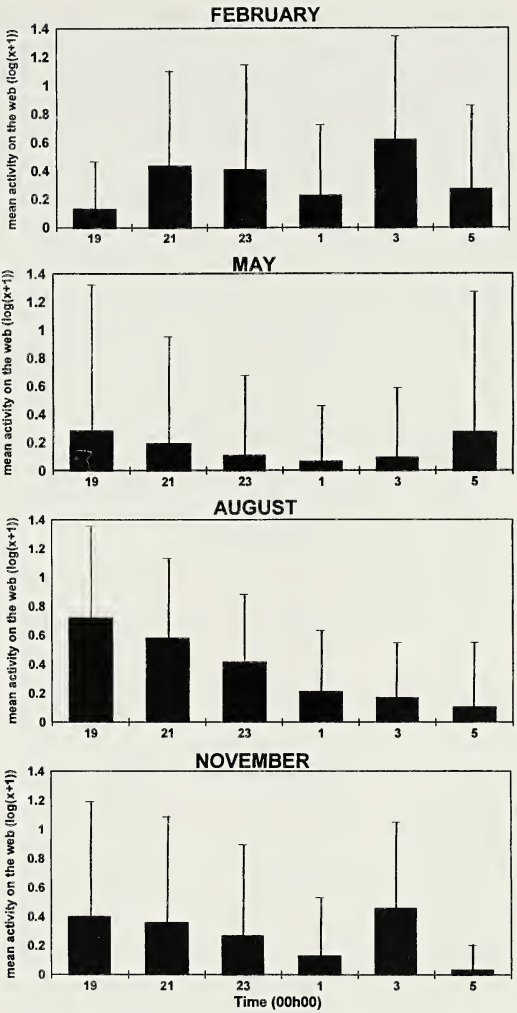


Figure 6.—Mean number of spiders on the web at night \pm SD.

The difference in the growth rate of spiders during winter and summer months corresponds to the initial slow increase and the exponential phase, respectively, of a typical sigmoid growth curve. The food requirements of a colony are expected to be greatest during the period of exponential growth of juveniles, i.e., during early summer. Consequently, conditions should be more favorable for growth in the summer months. This was largely the case for the abiotic conditions as well as the availability of prey.

Abiotic conditions: In May and August, mean nest temperatures were below 25 °C during the day and less than 15 °C at night. February was the hottest month and in both

Table 3.—Correlations (Pearson's) between mean number of spiders responding to prey stimulus (foraging), insects trapped on 40–60 webs (prey), nocturnal activity on the web (On web), wind and ambient temperature (T_{amb}). the following symbols have been used: only one prey item was recorded in night samples and therefore omitted from the analysis (*), appropriate for nocturnal data only (**), activity on the web was not included in the analysis of foraging response (***), significant partial correlations coefficient ($P \leq 0.05$)(§).

		Correlation coefficient (P -value)			
		Wind	T_{amb}	Prey	On Web**
February					
Day ($n = 15$)	Foraging	−0.054 (NS)	−0.387 (NS)	0.652§ ($P < 0.01$)	—
	Prey	−0.040 (NS)	−0.506§ ($P \leq 0.05$)	—	—
Night* ($n = 6$)	Foraging	−0.824§ ($P < 0.05$)	−0.479 (NS)	—	0.526 (NS)
	On Web	−0.503 (NS)	−0.371 (NS)	—	—
May					
Day ($n = 14$)	Foraging	−0.467§ ($P = 0.09$)	0.161 (NS)	0.046 (NS)	—
	Prey	−0.253 (NS)	−0.472 (NS)	—	—
Night ($n = 12$)	Foraging	0.356 (NS)	0.497 (NS)	0.493 (NS)	0.493 (NS)
	Prey	0.215 (NS)	0.429 (NS)	—	—
	On Web	0.438 (NS)	0.267 (NS)	0.348 (NS)	—
August					
Day ($n = 15$)	Foraging	−0.036 (NS)	0.050 (NS)	0.077 (NS)	—
	Prey	−0.182 (NS)	−0.188 (NS)	—	—
Night* ($n = 12$)	Foraging	0.421 (NS)	0.955§ ($P < 0.001$)	—	0.898 ($P < 0.001$)
	On Web	0.476 (NS)	0.961§ ($P < 0.001$)	—	—
November					
Day ($n = 18$)	Foraging	−0.529§ ($P \leq 0.05$)	−0.452§ ($P \leq 0.05$)	0.326 (NS)	—
	Prey	−0.349 (NS)	0.074 (NS)	—	—
Night ($n = 6$)	Foraging***	0.098 (NS)	0.516 (NS)	0.472 (NS)	—
	Prey	0.294 (NS)	0.829§ ($P \leq 0.05$)	—	—
	On Web	0.095 (NS)	0.431 (NS)	0.399 (NS)	—

February and November nighttime temperatures rarely fell below 20 °C. Although the nests were positioned on an exposed bridge, strong winds were not recorded during our observation periods. The windspeed was generally lower in the winter months of May and August and higher during November, both during the day and night. Nest and ambient temperatures peaked between 1200–1400 h and were lowest just before dawn. While the difference between day and nighttime nest temperatures was often > 15 °C during the winter months, in November there was little

difference between the maximum and minimum nest temperatures recorded (± 5 °C).
Temperatures inside the nest were nearly always higher than ambient, as found also by Seibt & Wickler (1990). Thus, in the summer months, spiders inside the nest might suffer excessive heat loads during mid-day, but they can cool convectively by moving out of the nest. Convective cooling may be enhanced by the prevalence of stronger afternoon winds during the summer months. Seibt & Wickler (1990) showed that *S. mimosarum* actively avoided temperatures above 41 °C. During

one hot day in December 1997, when ambient temperature exceeded 42 °C at 0900 h, we observed spiders moving onto the web into the shadow cast by the nest, and some females moved their egg sacs onto the web as well. This behavior was observed frequently in the social *S. dumicola* (Seibt & Wickler 1990; pers. obs.). A similar response to high mid-day nest temperatures occurs in the solitary *Stegodyphus lineatus* (Henschel et al. 1992) and in a widow spider *Latrodectus revivienis* (Lubin et al. 1993), both web-building species of desert habitats. In all of these cases, the silken structure of the nest does not protect the spiders from high daytime temperatures (see also Seibt & Wickler 1990), rather the spiders must use behavioral methods of thermoregulation.

Prey availability: Although insect abundance was highest during the day, the response of spiders to web vibrations (simulated prey) was greater at night. Furthermore, spiders handled a greater proportion of insects trapped at night than during the day. Nocturnal insects constituted only 8% of the total number of insects available on the web, but 47% of the prey actually handled by the spiders. The distribution of insect sizes suggests an explanation for this anomaly: more than half of the diurnal insects trapped were very small (< 3 mm body length), whereas more than half of the nocturnal insects were > 6 mm. Using an approximate conversion for insect body length to biomass (mass = $0.0305 \times \text{length}^{2.62}$; Rogers et al. 1976), we estimated that nocturnal insects constituted 28% of the biomass of available prey and 46% of the biomass of insects handled by the spiders. Thus, in terms of energy intake, nocturnal insects were more profitable than diurnal prey.

The prey taxa available changed throughout the year; and there were significant differences in the distribution of major taxa available in the web and those handled by the spiders, suggesting that the spiders fed selectively. Owing to the lack of independence between prey type and prey size in our data, we cannot determine whether selection was for particular types or size classes of prey, or both factors combined. Ward (1986) analyzed prey remains from nests of *S. mimosarum*, finding similar seasonal differences in composition as well as a predominance of large prey items (beetles and orthopteroid insects). Prey exoskeletons may

bias the results toward the larger insects, which are less likely to become fragmented. Thus, our observations of prey handled by the spiders confirm Ward's conclusion, that *S. mimosarum* preferentially takes large prey, even when most insects available are small.

Foraging activity as a function of climatic conditions and prey availability.—Both web maintenance and prey capture occurred mainly at night. This strong diel pattern of activity could not be explained by climatic conditions and prey availability alone. Another important factor might be the risk of predation or parasitism. From September to February substantial mortality occurred in colonies, largely from parasitism by *Pseudopompilus funereus* (Hymenoptera, Pompilidae) (pers. obs.). Predation by a Red-billed Woodhoopoe (*Phoeniculus purpureus*) was observed on a colony of *S. mimosarum* at a different site. Both of these predators are diurnal.

Ambient temperature played a direct role in foraging and web-maintenance activities, while wind appeared to have less of an influence. Humidity inside and outside the nest was not measured, but may influence activity as well. Typically, low humidity and high ambient temperatures would coincide during midday (see Seibt & Wickler 1990). High ambient temperatures during the day reduced foraging response, as did low nighttime temperatures. In August, the coldest month, there was little nocturnal activity. Similarly, in *S. lineatus*, both the speed and frequency of responses to a prey stimulus (tuning fork) was lower at low ambient temperatures (Henschel et al. 1992). Another solitary eresid, *Seothyra henscheli*, from the Namib desert, showed very limited foraging response at temperatures below 20 °C. In general, spiders adapted to hot climates, may be constrained more by low ambient temperatures than high ambient temperatures, especially if foraging activity is largely nocturnal, as is the case in *S. mimosarum*. However, above-ambient temperatures inside the nest at night may act to buffer the low ambient temperature and thereby increase the time available to the spiders for foraging activity in cold winter months. Furthermore, large nests with greater thermal mass are better buffered against low temperature effects (Weldon 1997). Small colonies and newly established nests, however, may be sensitive to

immediate climatic conditions, as well as to the indirect effects of climate on prey availability.

One of the consequences of low temperatures at the start of the post-winter growth phase is its potential to delay maturation. In the solitary *S. lineatus*, delayed maturation has a strong negative effect on fitness, as the occurrence of wasp parasitism increases with time in the season and juvenile survival decreases if emergence is delayed (Henschel et al. 1992; Schneider & Lubin 1997; Ward & Lubin 1993). In the latter species, the width of the window of time for development is determined by climatic factors. Long-term monitoring of changes in numbers and sizes of colonies of *S. mimosarum* will provide information on the extent to which growth and survival vary with changing biotic and abiotic conditions.

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THE IMPACT OF HABITAT FEATURES ON WEB FEATURES AND PREY CAPTURE OF *ARGIOPE AURANTIA* (ARANEAE, ARANEIDAE)

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ABSTRACT. Prey capture by the orb-web spider, *Argiope aurantia* Lucas 1833, depends on the type of the web-site selected. I analyzed *A. aurantia* web sites in open field and adjacent forest edge habitats to identify habitat features associated with web characteristics and prey capture. In the open field, the use of herbs or grass for web attachment was associated with smaller web diameters, and lower attachment heights and web heights. In both forest edge and open field, the distance to the nearest flower was less when web attachments were on composites. In the open field, webs attached to grass captured more orthopteran prey, and webs attached to herbs and composites captured more hymenopteran prey. The mean number of prey captured and the proportion of hymenopteran prey increased with higher web attachments in the open field habitat. Close proximity of webs to goldenrod in bloom in the open field habitat increased the mean number of prey captured and the proportion of hymenopteran prey. In the forest edge habitat, the presence of goldenrod was associated with more hymenopteran and orthopteran prey and with a higher mean prey number captured. Generally, webs in the open field habitat had more hymenopteran and orthopteran prey and higher mean prey number captured than the forest edge habitat. The web-site providing the greatest probability for encountering and capturing prey is predicted to be one with a tall composite plant for web attachment near goldenrod in bloom.

Keywords: Habitat selection, old-field habitat, predation, web-site

Web building spiders can increase prey capture by selecting sites providing high prey availability (Turnbull 1973; Riechert 1976; Riechert & Luczak 1982; Bradley 1993). Many factors determine web-site quality including thermal stress on the spider (Riechert & Tracy 1975; Tolbert 1979), web structure (Colebourn 1974; Greenstone 1984), and prey availability (Olive 1980; Howell & Ellender 1984). Web-site quality could be determined by habitat features of the web-site that influence prey encounter and capture. Therefore, a spider may select a high quality web-site by choosing habitat features associated with high prey capture rate.

Differences in habitat use can change a spider's diet (Brown 1981; Horton & Wise 1983) by changing prey availability (Olive 1980, 1981a, 1981b, 1982) and/or web characteristics (Greenstone 1984). If flowers in bloom attract insect pollinators to a habitat, then flowers close to a web-site can increase pol-

linators (e.g., Hymenoptera) encountering the web (see Howell & Ellender 1984; McReynolds & Polis 1987).

Two habitat features that influence important web characteristics are the type and height of plant used for web attachment (Enders 1973, 1975; Pasquet 1984). If sturdy plants such as trees and shrubs support larger stronger webs, then larger, more powerful prey items (e.g., Orthoptera) can be captured compared to webs on slighter plants such as grasses (Uetz et al. 1978; McReynolds & Polis 1987). If the flying insects (e.g., Hymenoptera) are at greater heights in vegetation where there is more open space for flight, then increasing the height of plant used for web attachment (thus increasing web height) can increase encounters with the web by flying insects (McReynolds & Polis 1987).

For habitat selection to be effective, different habitats or microhabitats must differ in effect on individual fitness, and the individual must be able to select the higher quality habitat based on some environmental cue or cues (Orians & Wittenberger 1991). However, temporal and spatial variations in habitat quality

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make it difficult to find and choose a high quality site (Orians & Wittenberger 1991), and the risk of movement from a web site increases the expediency of remaining in a lower quality site (Vollrath 1985). *Argiope aurantia* must select a web-site ensuring a high prey encounter rate in a heterogeneous old-field habitat with spatial variation in vegetation and flowers in bloom and temporal variation of flowers blooming and prey availability.

This paper describes associations between habitat features and estimates of prey capture for the orb-web spider, *A. aurantia*. The four habitat features considered were: plant type for web attachment, web attachment height on plant, nearest flower in bloom and nearest flower distance to web. In a heterogeneous environment of an old-field, these habitat features are possible cues for the spider to select a web-site with a high probability of prey capture. The plants chosen for web attachment could be the most influential habitat feature for the spider building a web. Therefore, a comparison among the various plant types chosen by spiders for the highest web attachment with other habitat features and web characteristics of *A. aurantia* could help establish associations. The main questions I address are: How do vegetative habitat features influence *A. aurantia*'s web characteristics and the number and type of prey captured? What habitat features are potential cues that could be used by the spider during web-site selection to choose a web-site with high probability of future prey capture?

METHODS

Study animal.—*Argiope aurantia* builds a large vertical orb-web on vegetation in old-field habitats. The diurnal spider then sits at the web hub to wait for prey snared in the web (Reed et al. 1969). Spiders capture large prey encountering the web by wrapping the prey in silk before delivering a bite (Robinson 1969; Robinson et al. 1969; Hardwood 1974). Wrapped prey remain on the web until carried to the hub for feeding. The female spiders reach maturity and produce eggs in September and October (Olive 1980; Horton & Wise 1983). The spiderlings survive the winter in the egg sac and emerge in April and May (Tolbert 1977).

Habitat.—Habitat utilization by adult female *A. aurantia* was investigated from 4 Sep-

tember–1 October 1989, 22 September–25 October 1990, 14 September–13 October 1991, and 13 September–17 October 1992 in early successional old-field habitats located on the property of Blue Mountain College, Blue Mountain, Mississippi (1 km N of Blue Mountain on Tippah County Road 805). I divided the old-field into two habitats, open field and forest edge. Open field habitat was old pastures, and forest edge habitat was the margin between woods and mowed lawns for a softball field and golf course. Both habitats had a mixed grass-herbaceous vegetation of an early successional stage. The herbaceous vegetation included many species that bloom in the late summer and early autumn, such as goldenrod (*Solidago* spp.), boneset (*Eupatorium perfoliatum*), ironweed (*Vernonia* sp.), fleabane (*Erigeron* spp.), sunflower (*Helianthus* spp.), other composites (Asteraceae), honeysuckle (*Lonicera japonica*) and partridge pea (*Cassia* sp.). Shrubs (e.g., blackberry, *Rubus* sp. and pasture rose, *Rosa* sp.) and some early successional trees (e.g., sweetgum, *Liquidambar styraciflua*; *Sassafras albidum*; and sumacs, *Rhus* spp.) were also common in both habitats. Willows (*Salix* sp.) occurred in a boggy area of the open field. The two habitats mainly differed in the presence of canopy trees. The open field had saplings of early successional trees but very few large trees to shade the other vegetation, while the forest edge had canopy trees shading the grass-herbaceous vegetation daily.

Data collection.—Habitat and web characteristics of adult female *A. aurantia* spiders were gathered by walking through the open field or along the forest edge and finding a spider at the web hub. This search was not considered to be a census of the spider population in either habitat. The animals were collected in batches, uniquely marked on the dorsal abdomen with a permanent marker, and released within 24 hours on vegetation of the open field or forest edge habitat. The marked spiders were found on a web after release and observed as long as they remained at the web-site. Foraging data were collected by observing captured and wrapped prey in the web. If the web-site was abandoned, attempts were made to find again the marked spider and continue to record data at the new web-site. Foraging data were collected at several web-sites at one time for a total of 88 web-sites in the

forest edge and 57 web-sites in the open field. Additional data were collected on web and habitat characteristics from spiders that escaped collection for marking, were not found again after mark and release, or were found later near marked spiders.

Habitat and web parameters measured were: (1) the plant used for the highest web attachment point (grass, composite, herb, shrub, or tree), (2) web attachment height on that plant, (3) taxon of nearest flower in bloom to the web hub (goldenrod, boneset, ironweed, fleabane, sunflower, other composites, honeysuckle, or partridge pea) or, if no flower was within four meters, then recorded as "no flower," (4) distance from nearest flower blossom to the web hub, (5) web height at the orb hub, and (6) vertical web diameter. Ironweed, fleabane, sunflower, boneset, and other composites were pooled into "composite flower" class in the forest edge habitat, and honeysuckle and partridge pea were pooled into "other flower" class. In the open field habitat, all flowers except goldenrod and boneset were pooled into the "other flower" class.

Foraging data were collected by observing webs of marked individuals between 1600–1900 h to record any prey wrapped (i.e., captured) by the spider during the day. Foraging variables for each marked individual included: (1) number of wrapped prey present in the web, (2) prey taxon, and (3) prey size (length of body and width of abdomen). The mean number of days of collecting foraging data of marked individuals at a particular web-site was 2.6 days in the forest edge and 5.6 days in the open field. The mean prey number captured per day for each marked individual could then be calculated. I identified to order each prey item while on the web and measured the length when the condition of the remains allowed. Orthoptera and Hymenoptera had the highest proportions, with other insect orders (Coleoptera, Diptera, Lepidoptera, Hemiptera, Homoptera, Odonata, and Mecoptera) and arachnid orders (Araneae and Opiliones) pooled into "other prey" class because of low numbers expected in contingency tables. To reduce disturbance to the spider, prey items were not removed from the web. Unidentifiable prey were pooled with "other prey" class.

Data analyses.—Comparisons between certain habitat features and other habitat fea-

tures, web characteristics, and spider prey capture were performed. Comparisons of relative proportion in a contingency table of a habitat feature and prey taxa captured used the adjusted *G*-test for independence. The data from individual spiders were pooled in habitat classes of the contingency table. Habitat classes or prey taxa classes were pooled when the assumption of expected values greater than five was violated. Comparisons of means were performed using analysis of variance (ANOVA) after using the Barlett's test (corrected) for homogeneity of variance test. If the class variances were heterogeneous, the Kruskal-Wallis test (corrected for ties) compared three or more classes and the Mann-Whitney *U*-test (corrected for ties) tested differences between two classes. Unplanned comparisons of a significant ANOVA were performed using the Student-Newman-Keuls Multiple Comparisons test (Sokal & Rohlf 1981). Associations between two variables were determined using a parametric test (product-moment correlation) if the assumption of linearity was not violated.

RESULTS

Plant types used for web attachment.—

In the forest edge, mean web attachment height, web height, and web diameter were not significantly different among plants used for web attachment (Table 1A). Nearest flower distance to the web was significantly different among those plants used for attachment in forest edge habitats and that distance was shorter with the web attached to a composite instead of grass, herbs, shrubs, or trees (Table 1A).

The mean web attachment heights of webs on grass and herbs were significantly lower than with shrubs, trees, and composites in the open field (Table 1B). Web heights were significantly different among the types of plants used for web attachment in the open field, with webs using shrubs higher than those using grass or herbs (Table 1B). Web diameters were also different among the types of plants used for web attachment in the open fields, with webs attached to composites larger than webs attached to herbs (Table 1B). In addition, the variances of nearest flower distance among web attachment plants in the open field were significantly heterogeneous; and the mean distance to the nearest flower was great-

Table 1.—Parameters associated with plant types for attachment of *Argiope aurantia* webs in forest edge and open field habitats. All mean values \pm standard error (SE). Means that are followed by the same letter are not significantly different (unplanned comparisons, $P < 0.05$).

	Mean attachment height (cm)	<i>n</i>	Mean hub height (cm)	<i>n</i>	Mean web diameter (cm)	<i>n</i>	Mean nearest flower distance (cm)	<i>n</i>
A. Forest edge								
Grass-Herbs	108.3 \pm 5.8	30	63.6 \pm 4.1	25	44.6 \pm 2.1	25	186.9 \pm 27.3a	16
Composites	118.1 \pm 10.6	16	62.1 \pm 5.0	12	38.8 \pm 2.9	12	38.8 \pm 19.5b	16
Shrubs	110.2 \pm 6.5	23	63.8 \pm 4.8	20	45.8 \pm 2.1	20	120.0 \pm 25.0a	20
Trees	124.6 \pm 5.3	54	69.0 \pm 3.9	49	48.1 \pm 2.1	48	133.2 \pm 14.2a	45
ANOVA	$F_{3, 119} = 1.61$ ns		$F_{3, 102} = 0.51$ ns		$F_{3, 91} = 2.00$ ns		$F_{3, 93} = 6.28$ $P < 0.001$	
B. Open field								
Grass	97.6 \pm 3.9ac	17	66.5 \pm 3.8a	17	40.6 \pm 2.8ab	17	109.4 \pm 23.6	18
Herbs	90.6 \pm 7.8a	9	57.5 \pm 4.6a	8	34.4 \pm 4.8a	8	55.7 \pm 22.7	7
Composites	121.8 \pm 7.3b	14	76.8 \pm 6.6ab	14	50.4 \pm 2.6b	14	25.4 \pm 16.2	14
Shrubs	127.5 \pm 6.2b	26	88.3 \pm 5.0b	26	42.9 \pm 2.4ab	26	103.5 \pm 26.5	24
Trees	130.0 \pm 9.7bc	6	75.0 \pm 8.3ab	6	50.0 \pm 7.0ab	6	75.0 \pm 18.9	6
ANOVA	$F_{4, 67} = 5.97$ $P < 0.001$		$F_{4, 66} = 4.34$ $P < 0.01$		$F_{4, 66} = 2.89$ $P < 0.05$			
Bartlett statistic							14.03, $P < 0.01$	
Kruskal-Wallis							12.98, $P < 0.05$	

er when the attachment plants were grasses or shrubs (Table 1B).

The diet in the web of marked *A. aurantia* was compared among the plants used for web attachment as the mean number of prey captured per day, the taxa of prey captured, and prey size of taxa. The mean prey numbers among classes of plants for web attachment were not significantly different at the forest edge (Table 2A) or in the open field (Table 2B). However, variances in mean prey number among classes of plants for web attachment were significantly heterogeneous for both habitats (Table 2). The proportions of prey taxa captured among the various attachment plants were significantly different for the open field but not for the forest edge (Fig. 1). In the open field, webs attached to herbs captured a higher proportion of hymenopteran prey and when attached to grass a higher proportion of orthopteran prey (Fig. 1B). The size of orthopteran prey among classes of plants for web attachment was not significantly different in either habitat (Fig. 2). Hymenopteran prey sizes and other prey sizes were significantly different among classes in the forest edge but not

in the open field (Fig. 2). For both hymenopteran prey and other prey, mean prey size was greater in the herb-grass than the tree-shrub class in the forest edge habitat though not as predicted. In a comparison among prey taxa, mean prey size of orthopteran prey was significantly larger than hymenopteran or other prey in the forest edge ($F_{2,61} = 29.0$, $P < 0.001$) and open field ($F_{2,167} = 109.6$, $P < 0.001$) (see Fig. 2).

Web attachment height.—Web characteristics and diet were compared to web attachment height in both habitats. Web height (in cm) was positively correlated with web attachment height (in cm) in forest edge ($y = 0.494x + 9.4$, $r^2 = 0.575$, $n = 102$, $F = 139.58$, $P < 0.001$) and open field ($y = 0.614x + 5.47$, $r^2 = 0.596$, $n = 71$, $F = 101.82$, $P < 0.001$). Web diameter (in cm) was positively correlated with web attachment height (in cm) in both habitats, but the relationship is not as strong for web diameter as web height in forest edge ($y = 0.171x + 25.9$, $r^2 = 0.256$, $n = 104$, $F = 35.1$, $P < 0.001$) and open field ($y = 0.152x + 25.9$, $r^2 = 0.124$, $n = 71$, $F = 9.77$, $P < 0.01$). A more

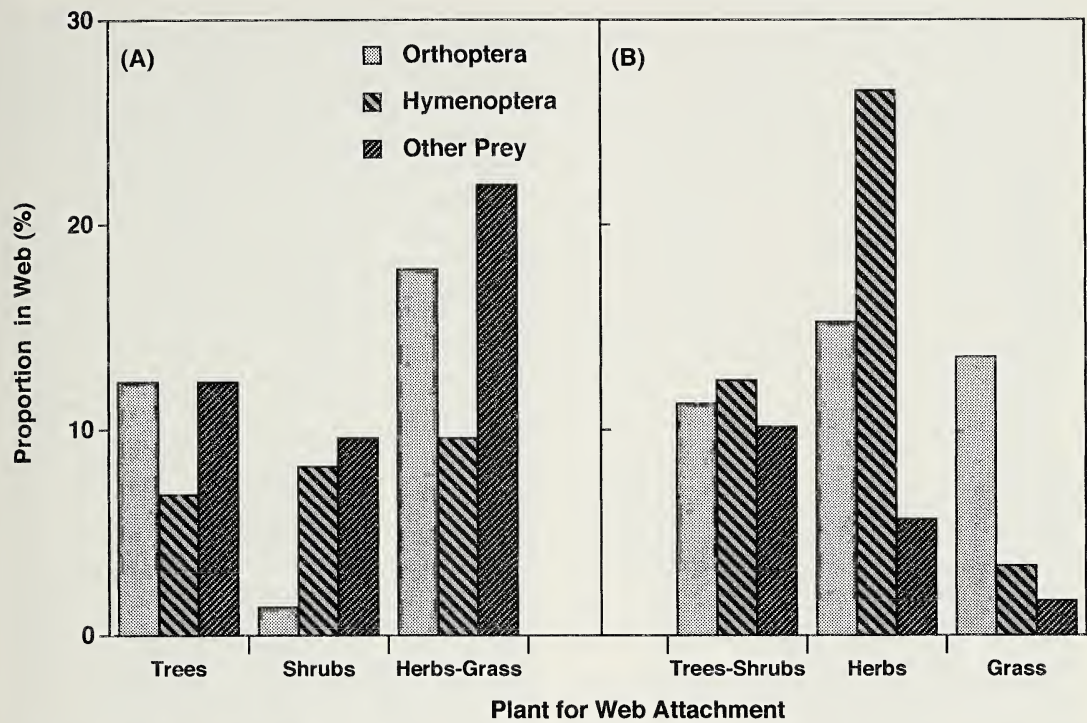


Figure 1.—The proportion (%) of prey taxa captured in the webs of *Argiope aurantia* among plant types for web attachment in two habitats. (A) In the forest edge, the frequency of prey taxa was not significantly different among classes ($G_{adj} = 6.53$, ns, $df = 4$, $n = 73$). (B) In the open field, the frequency of prey taxa was significantly different among classes ($G_{adj} = 26.13$, $P < 0.001$, $df = 4$, $n = 177$).

Table 2.—Mean prey number captured per day per individual *Argiope aurantia* for plant types for attachment of webs in forest edge and open field habitats.

	Mean	SE	n
A. Forest edge			
Herbs-Grass	0.32	0.08	23
Composites	0.61	0.15	14
Shrubs	0.64	0.25	14
Trees	0.28	0.08	36
Bartlett statistic		17.13, $P < 0.001$	
Kruskal-Wallis statistic	5.08, ns		
B. Open field			
Herbs	0.64	0.16	7
Grass	0.30	0.10	15
Composites	1.01	0.30	12
Shrubs	0.45	0.09	17
Tree	1.38	0.79	6
Bartlett statistic		39.74, $P < 0.001$	
Kruskal-Wallis statistic	8.16, ns		

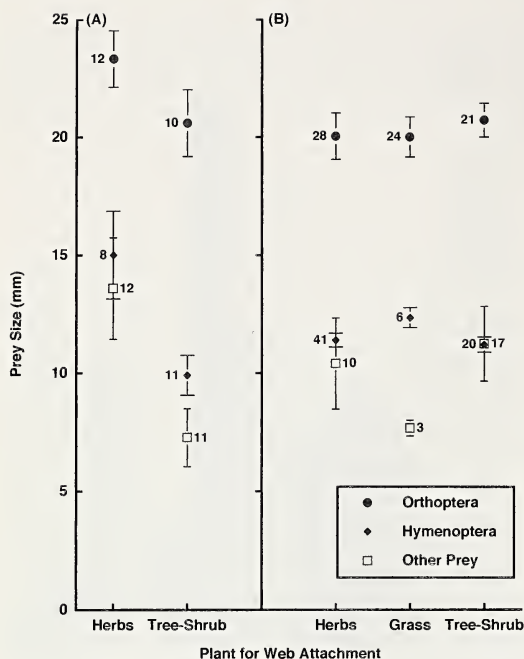


Figure 2.—The mean size (\pm SE, n) of orthopteran prey, hymenopteran prey, and other prey captured in the webs of *Argiope aurantia* among plant types for web attachment in two habitats. (A) In the forest edge, prey size was significantly different among classes for hymenopteran prey ($F_{1,17} = 7.48$, $P < 0.05$) and other prey ($F_{1,21} = 6.16$, $P < 0.05$) but not orthopteran prey ($F_{1,20} = 2.20$, ns). (B) In the open field, prey size was not significantly different among classes for orthopteran prey ($F_{2,70} = 0.19$, ns), hymenopteran prey ($F_{2,64} = 1.03$, ns), and other prey ($F_{2,27} = 0.44$, ns).

direct relationship between web attachment height and web height can exist because web attachment height determined the maximum web height, but web heights below maximum did occur. Web attachment height had a significant effect on these web characteristics but was not the only factor.

The observed diet of *A. aurantia* was compared among web attachment height classes as the number of prey captured per day per individual, and the taxa of prey caught. The mean prey number was not significantly different among web attachment height classes in the forest edge (Table 3A) but was in the open field, with the most prey captured in higher web attachments (Table 3B). The variances in prey number for web attachment heights were significantly heterogeneous for both habitats (Table 3). The proportions of

prey taxa captured among the web attachment height classes were not significantly different in the forest edge but were in the open field (Fig. 3) where higher webs captured a high proportion of hymenopteran prey and a low proportion of orthopteran prey (Fig. 3B).

Nearest flower.—The nearest flower in bloom was compared to spider diet in both habitats. The mean number of prey captured was significantly different among the four nearest flower classes in the forest edge, with lower number of prey captured per day with no flower near the web than with goldenrod nearby (Table 4A). There was no difference in mean number of prey captured among the three flower classes in the open field (Table 4B). The variances in prey number among nearest flower classes were significantly heterogeneous for both habitats with a high variance in prey number for the goldenrod class (Table 4). The proportions of prey taxa were significantly different among nearest flower classes in the forest edge and open field (Fig. 4). In the forest edge, the proportions of orthopteran and hymenopteran prey were higher with goldenrod nearby; but in the open field, the proportion of hymenopteran prey was higher with goldenrod, and orthopteran prey proportion was highest with the other flower class.

Nearest flower distance.—The nearest flower distance was compared to spider diet in both habitats. In the forest edge, mean number of prey captured was not significantly different between nearest flower distance classes of 0–50 cm and > 50 cm for any of the nearest flower taxa: goldenrod, composites, or other flowers (Table 5A). In the open field, only goldenrod had a significant difference in mean number of prey captured between nearest flower distance classes, with more prey caught by spiders near goldenrod than spiders > 50 cm from goldenrod (Table 5B). The proportions of prey taxa captured were not significantly different among the nearest flower distance classes for the forest edge but were significantly different for the open field (Fig. 5), with the proportion of hymenopteran prey increasing when the web was closer to a flower.

Habitat comparisons.—A measure of habitat quality was estimated by comparing spider diets between the two habitats. In the forest edge, the mean number of prey captured per day was significantly less (mean \pm SE = 0.40

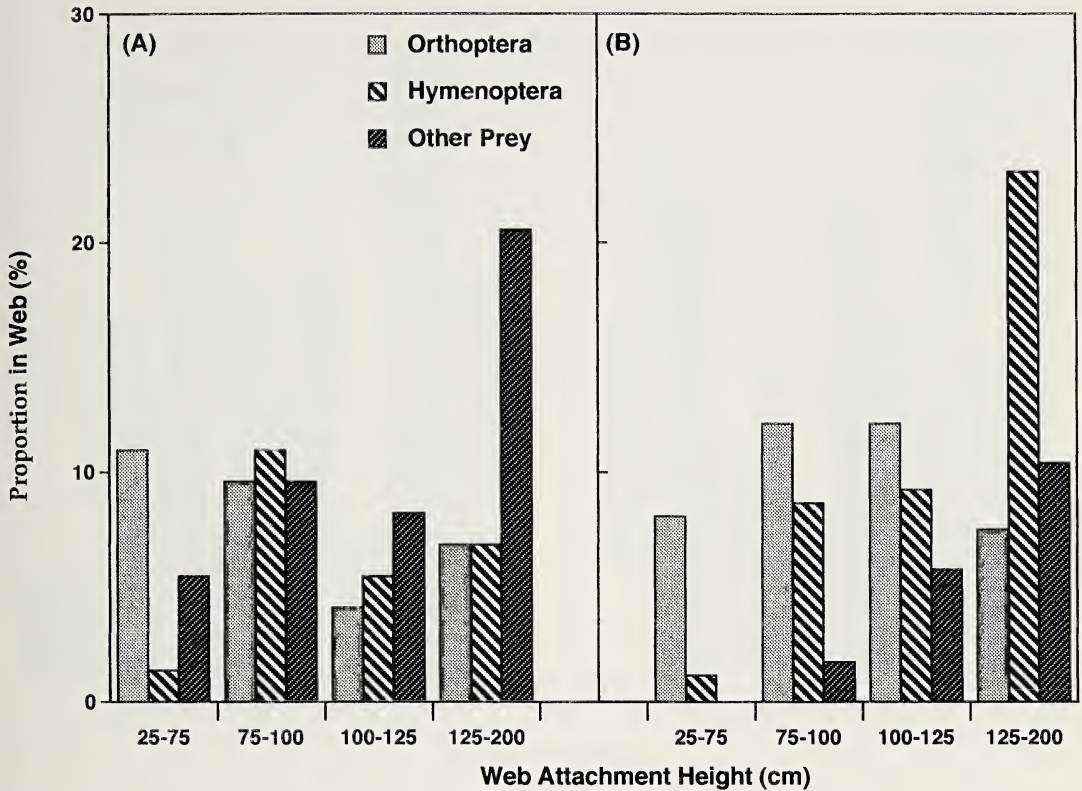


Figure 3.—The proportion (%) of prey taxa captured in the webs of *Argiope aurantia* among web attachment height classes in two habitats. (A) In the forest edge, the frequency of prey taxa was not significantly different among classes ($G_{adj} = 10.25$, ns, $df = 6$, $n = 73$). (B) In the open field, the frequency of prey taxa was significantly different among classes ($G_{adj} = 37.86$, $P < 0.001$, $df = 6$, $n = 173$).

Table 3.—Mean prey number captured per day per individual *Argiope aurantia* for web attachment heights in forest edge and open field habitats.

	Mean	SE	n
A. Forest edge			
50–100 cm	0.42	0.08	31
100–125 cm	0.42	0.16	23
125–150 cm	0.41	0.15	19
150–200 cm	0.31	0.11	14
Bartlett statistic		7.60, $P < 0.05$	
Kruskal-Wallis statistic	1.50, ns		
B. Open field			
50–100 cm	0.44	0.08	16
100–125 cm	0.49	0.17	24
125–200 cm	1.11	0.29	16
Bartlett statistic		19.62, $P < 0.001$	
Kruskal-Wallis statistic	9.66, $P < 0.01$		

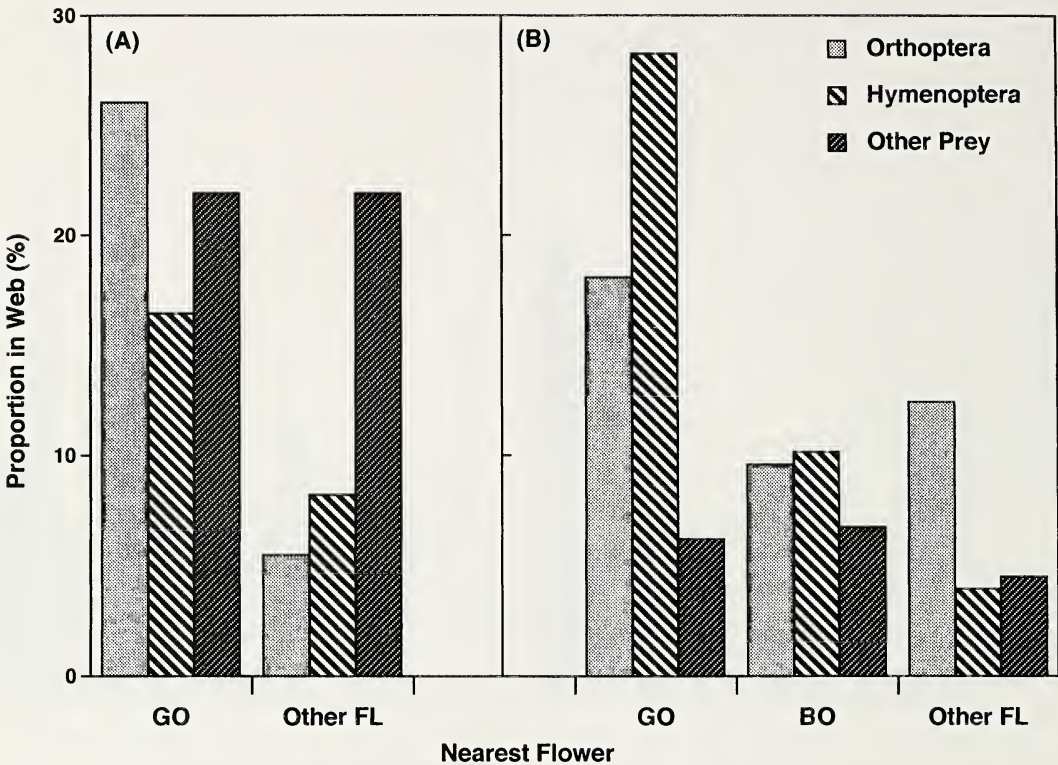


Figure 4.—The proportion (%) of prey taxa captured in the webs of *Argiope aurantia* among nearest flower classes in two habitats. (A) In the forest edge, the frequency of prey taxa was significantly different among classes ($G_{adj} = 6.37, P < 0.05, df = 2, n = 73$). (B) In the open field, the frequency of prey taxa was significantly different among classes ($G_{adj} = 16.4, P < 0.01, df = 4, n = 177$). Abbreviations: BO = boneset, GO = goldenrod, Other Fl = other flowers.

Table 4.—Mean prey number captured per day per individual *Argiope aurantia* for nearest flower in bloom in forest edge and open field habitats.

	Mean	SE	n
A. Forest edge			
Composite Flowers	0.37	0.11	26
Goldenrod	0.53	0.12	32
Other Flowers	0.51	0.16	14
No Flower	0.08	0.06	16
Bartlett statistic		13.71, $P < 0.01$	
Kruskal-Wallis statistic	5.08, $P < 0.01$		
B. Open field			
Boneset	0.54	0.14	16
Goldenrod	0.80	0.24	20
Other Flowers	0.59	0.19	21
Bartlett statistic		6.96, $P < 0.05$	
Kruskal-Wallis statistic	1.05, ns		

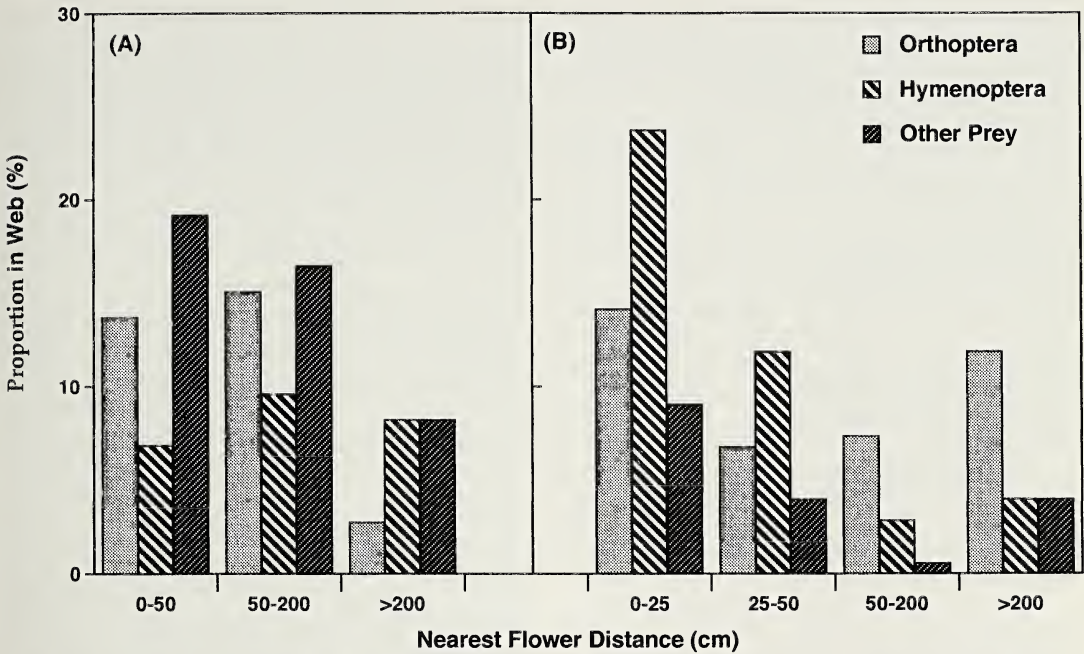


Figure 5.—The proportion (%) of prey taxa captured in the webs of *Argiope aurantia* among nearest flower distance classes in two habitats. (A) In the forest edge, the frequency of prey taxa was not significantly different among classes ($G_{adj} = 4.34$, ns, $df = 4$, $n = 73$). (B) In the open field, the frequency of prey taxa was significantly different among classes ($G_{adj} = 20.26$, $P < 0.01$, $df = 6$, $n = 177$).

± 0.06 , $n = 88$), than in the open field (0.65 ± 0.12 , $n = 57$) ($U = 1924.0$, $P < 0.05$). The variances in prey number between habitats were significantly heterogeneous ($F = 2.33$, $df = 56, 87$, $P < 0.001$). The proportions of prey taxa captured were significantly different between the two habitats (Fig. 1, $G_{adj} = 18.51$, $df = 2$, $P < 0.001$), with the proportions of both hymenopterans and orthopteran prey higher in the open field. Therefore, the forest edge habitat had lower quality prey capture sites for *A. aurantia* than the open field.

DISCUSSION

A possible explanation for the difference in prey capture between the two habitats is the differences in the relative density of grass and herbaceous vegetation affecting prey availability (Olive 1980, 1981a) and/or the presence of flowers in bloom that attract *A. aurantia* prey. The two habitats also differ in abiotic environmental factors (e.g., the presence of shade) that could influence the spider directly or through prey availability (Riechert & Tracy 1975). Enders (1973) observed that *A. aurantia* shifts from closed sites with pe-

rennials (description similar to the forest edge habitat) to open sites (i.e., open field) as they enter adulthood. However, more adult *A. aurantia* in this study remained in the forest edge habitat because mowed lawns could act as a barrier to their movement.

Habitat utilization can determine the structure and size of the web (Colebourn 1974; Pasquet 1984; Lubin et al. 1993). Web height at the hub influenced the diet of *A. aurantia* through an increase in the proportion of Hymenoptera and a decrease in Orthoptera captured as the prey capturing surface was positioned higher (McReynolds & Polis 1987). The present results are consistent: a similar association was found between web attachment height and proportions of prey taxa, and a positive correlation existed between web attachment height and web height. This increase in web attachment height was also associated with increased prey capture. Maybe spiders select web-sites providing high web attachments to increase web height. This, in turn, increases the frequency of encounter and capture of higher flying Hymenoptera and increases the total number of prey captured

Table 5.—Mean prey number captured per day per individual *Argiope aurantia* for distance to nearest flower in bloom of different flower types in forest edge and open field habitats.

	Mean	SE	n	Mann-Whitney <i>U'</i>
A. Forest edge				
Composite Flowers				
0–50 cm	0.42	0.20	11	<i>U'</i> = 72.0
>50 cm	0.24	0.11	12	<i>P</i> = 0.73, ns
Goldenrod				
0–50 cm	0.6	0.19	11	<i>U'</i> = 131.5
>50 cm	0.37	0.09	20	<i>P</i> = 0.38, ns
Other Flowers				
0–50 cm	0.64	0.17	6	<i>U'</i> = 28.5
>50 cm	0.46	0.29	7	<i>P</i> = 0.29, ns
B. Open field				
Boneset				
0–50 cm	0.6	0.12	10	<i>U'</i> = 44.5
>50 cm	0.43	0.32	6	<i>P</i> = 0.12, ns
Other Flowers				
0–50 cm	0.69	0.48	8	<i>U'</i> = 42.5
>50 cm	0.67	0.13	7	<i>P</i> = 0.09, ns
Goldenrod				
0–50 cm	1.32	0.43	10	<i>U'</i> = 89.5
>50 cm	0.28	0.08	10	<i>P</i> < 0.01

(McReynolds & Polis 1987). However, these results do not support the prediction that sturdier plants used for web attachment support stronger, larger webs and therefore capture larger and stronger prey such as orthopterans.

The presence of flowers near the web site may directly affect prey capture of *A. aurantia* by attracting insect pollinators, herbivorous insects, and their arthropod predators. Results suggest that proximity to goldenrod increases prey capture probability more than any other flower. In both habitats, Hymenoptera were captured near goldenrod, maybe because this plant attracts more insect pollinators than other flowers in old-field habitats during late summer and autumn. In the forest edge, the capture of Orthoptera also increased near goldenrod, maybe because goldenrod with associated grass or herbaceous vegetation also attracts more herbivorous insects than the trees and shrubs that are common at the forest edge. Nearest flower and nearest flower distance appear to be good indicators of prey capture and may be predictors of prey avail-

ability and web-site quality, although nearest flower and nearest flower distance do not indicate the presence and density of other flowers in bloom near the web site. Further research is required to test the above predictions on the effect of goldenrod on prey availability and web-site quality.

Prey capture at a web-site can fluctuate (Janetos 1982; Bradley 1993; Vollrath 1985), and the risk to a spider in selecting a web-site can increase with temporal and/or spatial variation in prey availability (Caraco & Gillespie 1986; Gillespie & Caraco 1987; Smallwood 1993). The data on within web-site variance needed to evaluate the decisions made by individual spiders on their tenure at web-sites (see Caraco et al. 1995) are not available in this paper. However, when based on the between web-site variance, web-site quality is highly variable within habitat classes (e.g., high mean and variance of prey number in the goldenrod class of the open field habitat). One explanation for spatial and temporal variability among web-sites is that attractiveness of the flowers to insect pollinators around the web-site changes over time, changing prey availability at various web-sites. These hypotheses need further testing.

The predicted high quality web-site for *A. aurantia* (i.e., one that shows a high mean prey number) is a combination of habitat features including a tall (> 125 cm) plant for web attachment near (< 50 cm) goldenrod in bloom. However, with the high variance, there is a risk that an individual will not capture the minimum energy requirements. Caraco et al. (1995) predict that solitary spiders such as *A. aurantia* should be more risk-prone by selecting highly variable foraging sites because these places would occasionally yield sufficient energy for survival and reproduction while less variable (with the average below the minimum) sites rarely or never yield sufficient energy. Therefore, a spider should select a web-site with certain habitat features—not to ensure constant prey availability—but to increase the probability of occasional high prey capture. In addition, selection of a web-site by *A. aurantia* with the above habitat features should increase the probability of sufficient prey capture for survival and reproduction. The major emphasis of further research is to establish whether *A. aurantia* does select or prefer web-sites with these predicted habitat features.

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EVALUATION OF FORMULAE TO ESTIMATE THE CAPTURE AREA AND MESH HEIGHT OF ORB WEBS (ARANEOIDEA, ARANEAE)

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ABSTRACT. We evaluated several formulae to estimate the capture area (the area of the web covered by capture spirals) and the mesh height (the distance between capture spirals) of orb webs constructed by *Argiope keyserlingi* Karsch. The accuracy of the various formulae was estimated through regression analyses. Accordingly, we propose two new formulae specifically suited for asymmetric orb webs, which provide accurate estimates of capture area and mesh height.

Keywords: Web architecture, web design, Araneidae, *Argiope keyserlingi*

The fundamental unit of behavior in orb-web spiders is the construction and design of the web. Web size and design can vary due to prey size (Sandoval 1994), food availability (Herberstein et al. 2000; Sherman 1994; Tso 1999), developmental stage (Higgins 1995; Heiling et al. 1998; Heiling & Herberstein 1998), physiological status (Eberhard 1988), web site (Eberhard 1989) and various abiotic factors (Vollrath et al. 1997). These web variations can directly influence the number and types of prey entangled. For example, a larger web will increase the rate of prey interception (Chacón & Eberhard 1980; Higgins & Buskirk 1992; Herberstein & Elgar 1994). Similarly, the distance between the capture spirals (mesh height) may affect the visibility of the web (Rypstra 1982; Craig 1986) and the size of prey entangled (Uetz et al. 1978; Murakami 1983; Miyashita & Shinkai 1995; Herberstein & Heiling 1998).

While the geometric nature of orb webs aids the measurement and consequent comparison of web elements such as web size and mesh height, these are sometimes difficult to obtain, particularly in the field. Therefore, some studies have used the length of the web radius (Higgins & Buskirk 1992) or web diameter (McReynolds & Polis 1987) as a very rough approximation of web size. Several recent studies have estimated web area with the help of formulae that require only a few measurements of the web (e.g., Nentwig 1985;

Walker 1992; Sherman 1994). Regrettably, those studies do not provide a detailed description of the formulae used, nor do they estimate the accuracy of the generated values.

Recently Tso (1996) investigated the orb webs of *Argiope trifasciata* Forskål 1775 and estimated the capture area of the web (= the area covered by sticky spirals) and the mesh height using two formulae. Despite the detailed description of these formulae, Tso (1996) did not provide an account of how accurate the estimates were. Here we test the accuracy of several formulae to estimate capture area and mesh height by comparing the values derived from the formulae with exact values. Those tests will help validate surrogate variables and provide ecologists and ethologists with appropriate tools for estimating orb web parameters in the field.

METHODS

We used the webs of 11 adult female *Argiope keyserlingi* Karsch 1878 (built in 40 cm × 50 cm × 8.5 cm frames in the laboratory). The spiders were collected from suburban gardens in Brisbane, Australia and transferred to the laboratory in Melbourne, Australia. Each spider constructed one web, which was used for analysis ($n = 11$). Exact mesh height was obtained by measuring each distance between the spirals in the vertical upper and lower sector (Fig. 1). The values for both the upper and lower web halves were averaged for the mesh

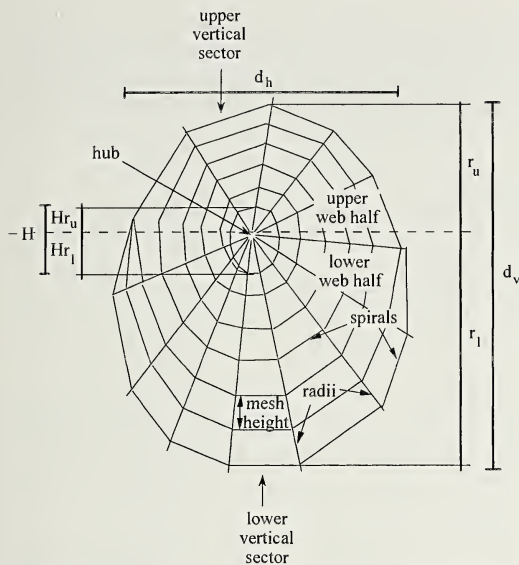


Figure 1.—A schematic representation (modified from Heiling & Herberstein 1998) of an asymmetric orb-web, defining the parameters used in the equations given by Tso (1996) and in this study. See text for symbols used.

height of the whole web. The exact capture area was obtained by summing the area covered by spirals in each web sector. The individual sector areas were calculated by treating each sector as a trapezoid, where the inner- and outermost spirals were assumed parallel. Although the inner and outer spirals may not always be perfectly parallel, we expect the consequent biases to be minimal. The exact capture area excluded the area of the hub, which is not covered by sticky spirals and therefore does not function in capturing prey.

To estimate the capture area of the webs, we considered several scenarios, which differed in the number of measurements taken from the webs. For example, a researcher may only know a single web diameter or may know all four web radii and the hub radii. We then developed formulae that are based on the available information and tested their predictive powers.

The ‘Vertical Radii’ formula (a) assumes a circular approximation of the web and estimates the radius from the vertical web diameter (d_v), which extends from the outermost spiral in the upper web half vertically through the hub to the outermost spiral in the lower web half (Fig. 1). The hub area is included in this formula.

(a) $(d_v/2)^2\pi$

The ‘Vertical Radii – Hub’ formula (b) estimates the ‘true’ capture area by subtracting the hub area, which is calculated using the vertical hub diameter (H). This diameter extends vertically from the innermost spiral in the upper web half to the innermost spiral in the lower web half (Fig. 1).

(b) $(d_v/2)^2\pi - (H/2)^2\pi$

The ‘Ellipse’ formula (c) assumes an elliptical approximation of the web and estimates both radii from the vertical and the horizontal diameter (d_h), respectively, but includes the hub area in its estimation. The ‘Ellipse – Hub’ formula (d) subtracts the hub area using the vertical hub diameter.

(c) $(d_v/2)(d_h/2)\pi$

(d) $(d_v/2)(d_h/2)\pi - (H/2)^2\pi$

The capture area formula (e; ‘Tso – Hub’) used by Tso (1996) calculates the web area of the upper and lower web halves separately using semi-circle approximations. It requires the upper (r_u) and lower (r_l) vertical radii, which extend from the hub to the outermost spiral in the upper and lower web half, respectively (Fig. 1). The area of the hub is calculated using the vertical hub diameter and subtracted to estimate the capture area.

(e) $\left[\frac{1}{2}\pi r_u^2 - \frac{1}{2}\pi \left(\frac{H}{2} \right)^2 \right] + \left[\frac{1}{2}\pi r_l^2 - \frac{1}{2}\pi \left(\frac{H}{2} \right)^2 \right]$

The ‘Adjusted Radii – Hub’ formula (f) is a modification of the ‘Tso – Hub’ formula. It also assumes a circular approximation treating each web half as semi-circles, but it adjusts the vertical radii by taking the horizontal diameter into consideration. Additionally, the hub area is calculated using the upper (Hr_u) and lower (Hr_l) hub radii separately. For this formula we required the upper and lower vertical radii, the horizontal diameter, the upper vertical hub radius and the lower vertical hub radius.

(f) $\left[\frac{1}{2}\pi r_{au}^2 - \frac{1}{2}\pi (Hr_u)^2 \right] + \left[\frac{1}{2}\pi r_{al}^2 - \frac{1}{2}\pi (Hr_l)^2 \right]$

Table 1.—The mean ± SE of the actual and the estimated capture area using various formulae which either include (+) or exclude (−) the area of the hub. The functional relationships between the actual and the estimated values are indicated using linear regression models with the SE of the regression slope given in parentheses. The *F* value indicates the significance of the regression model (Wilkinson 1992).

Estimate	Mean ± SE (cm ²) <i>n</i> = 11	Functional relationship	Significance
Actual capture area	555.8 ± 40.8		
Vertical Radii + Hub	628.2 ± 47.3	<i>y</i> = 207.9 + 0.6 (0.22) <i>x</i> ; <i>R</i> ² = 0.347	<i>F</i> = 6.3; <i>P</i> = 0.03
Ellipse + Hub	572.8 ± 33.6	<i>y</i> = −103.9 ± 1.2 (0.13) <i>x</i> ; <i>R</i> ² = 0.890	<i>F</i> = 82.2; <i>P</i> = 0.0001
Vertical Radii − Hub	547.2 ± 41.7	<i>y</i> = 206.2 + 0.6 (0.03) <i>x</i> ; <i>R</i> ² = 0.360	<i>F</i> = 6.6; <i>P</i> = 0.03
Tso − Hub	637.5 ± 48.5	<i>y</i> = 160.4 + 0.6 (0.19) <i>x</i> ; <i>R</i> ² = 0.493	<i>F</i> = 10.7; <i>P</i> = 0.01
Ellipse − Hub	491.9 ± 29.7	<i>y</i> = −96.8 + 1.3 (0.12) <i>x</i> ; <i>R</i> ² = 0.925	<i>F</i> = 124.5; <i>P</i> = 0.0001
Adjusted Radii − Hub	513.6 ± 30.7	<i>y</i> = −116.1 + 1.3 (0.08) <i>x</i> ; <i>R</i> ² = 0.965	<i>F</i> = 273.3; <i>P</i> = 0.0001

The adjusted upper (*r*_{au}) and lower (*r*_{al}) vertical web radii are:

$$r_{au} = \frac{r_u + \frac{d_h}{2}}{2}$$

$$r_{al} = \frac{r_l + \frac{d_h}{2}}{2}$$

We tested two different formulae to estimate the average mesh height in orb-webs. The first (g) was previously published by Tso (1996) and it requires the upper and lower web radii, the hub diameter and the number of sticky spirals in the upper (*S*_u) and lower (*S*_l) web halves counted in the vertical sector directly above and below the hub (Fig. 1).

(g)

$$\frac{1}{2} \left[\frac{\left(r_u - \frac{H}{2} \right)}{S_u} + \frac{\left(r_l - \frac{H}{2} \right)}{S_l} \right]$$

We modified this formula (h), using the upper and lower vertical hub radii rather than the hub diameter.

(h)

$$\frac{1}{2} \left(\frac{r_u - Hr_u}{(S_u - 1)} + \frac{r_l - Hr_l}{(S_l - 1)} \right)$$

The formulae for capture area and mesh height were evaluated using regression analyses between exact values and their equivalent estimates generated by the formulae. Accordingly, an accurate estimate generates a high correlation coefficient (*R*²). All analyses were

performed using SYSTAT 5.2 for the Macintosh (Wilkinson 1992).

RESULTS AND DISCUSSION

Generating the capture area from the vertical diameter alone does not yield accurate estimates (Table 1). In contrast, estimates calculated by the ‘Ellipse’ formula are greatly improved. This is most likely to be due to the asymmetric nature of *A. keyserlingi* webs and indeed many other orb webs (Vollrath & Morén 1985; Vollrath 1987; Foelix 1992; Herberstein & Heiling 1999). Generally, orb webs are vertically elongated, particularly in the lower web half and the horizontal radii are shorter. Thus considering the horizontal diameters will improve estimates for asymmetric webs. Subtracting the hub area from the ‘Vertical Radii’ and ‘Ellipse’ formulae further improved these estimates (Table 1). Thus excluding the area of the hub from a capture area estimate is warranted for *A. keyserlingi* and species with similar webs. In those species, however, where the hub only takes up a smaller proportion of the web, it may be of minor importance.

Despite incorporating more web parameters than the ‘Ellipse − Hub’ formula, the ‘Tso − Hub’ formula did not yield as accurate estimates (Table 1). This is primarily due to web asymmetry, which also affects the hub region. Consequently, the capture area is generally

Table 2.—The mean \pm SE of the actual and the estimated mesh height using formulae given in Tso (1996) and this study. The functional relationships between the actual and the estimated mesh height are indicated using linear regression models with the SE of the regression slope given in parentheses. The F value indicates the significance of the regression model (Wilkinson 1992).

	Mean \pm SE (cm) $n = 11$	Functional relationship	Significance
Actual	0.45 \pm 0.02		
Tso (1996)	0.39 \pm 0.02	$y = 0.13 + 0.83 (0.17) x$; $R^2 = 0.66$	$F = 19.96$; $P = 0.002$
This study	0.45 \pm 0.02	$y = 0.02 + 0.95 (0.07) x$; $R^2 = 0.95$	$F = 199.13$; $P = 0.0001$

overestimated, particularly in the lower web half. The most accurate estimates are generated by the ‘Adjusted Radii – Hub’ formula, because vertical asymmetry is being considered by incorporating the horizontal radii as well as calculating the upper and lower hub region separately (Table 1). Additionally, this formula generates separate values for the upper and lower web regions, which can be used for further analyses.

The mesh height formula used by Tso (1996) was not as accurate as our modified formula (Table 2) for two main reasons. First, Tso’s (1996) formula uses the vertical hub diameter rather than the upper and the lower vertical hub radii separately, which introduces a bias in asymmetric webs. Second, the sector length covered by the sticky spirals is divided by the number of spirals, a common mistake (e.g., Sandoval 1994). Instead, this length should be divided by the number of spacings between the spirals, which equals the number of spirals minus one. This is particularly important for webs with few spiral spacings. Obviously, the accuracy of a mesh height formula could be further improved by sampling and incorporating additional web sectors.

The appropriateness of any web formula largely depends on the geometric nature of the web. Circular approximations such as the ‘Vertical Radii – Hub’ or the ‘Tso – Hub’ formulae, may accurately estimate capture area in symmetric and circular webs. Asymmetric webs with large hub areas however require more complex approximations, such as the proposed ‘Adjusted Radii – Hub’ formula.

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**POPULATION STRUCTURE, SEASONALITY, AND
HABITAT USE BY THE GREEN LYNX SPIDER
PEUCETIA VIRIDANS (OXYOPIDAE) INHABITING
CNIDOSCOLUS ACONITIFOLIUS (EUPHORBIACEAE)**

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ABSTRACT. For one year we studied the habitat use of *Peucetia viridans* living on *Cnidoscolus aconitifolius*, in a pasture land in Mérida, Yucatán, México. Highest spider density was recorded in August (total 118, adults 77), and lowest in May (total 7, adults 2). Spider density was significantly higher in isolated plants and lower in plants in a patch. Sex ratio (♀:♂) varied from 1:1.5 in April, to 1:1 in May, and to 1:0.1 in September. The dominant instar (both sexes) changed during the study. Throughout the study more spiders were recorded in 'repose' than performing any other activity. Foraging and feeding were more intense between July and September, when their prey, flower visitors, were more abundant. The number of spiders on plants varied spatially and temporally due to the combined effects of distance of the individual plant to the nearby forest, monthly precipitation, plant height, and number of panicles in anthesis. Forty-eight percent of the spiders were found living on plants with 20–30 panicles in anthesis (2% of the plant population). Most of the spiders (except for adult females) were found either below or above leaves. There were no significant differences in the distribution of most stadia respective to plant height. Positive significant correlations were found between the number of spiders and the abundance of floral visitors when the data were compared shifted-back one month, and between the number of spiders and the number of panicles in bloom when the data were compared shifted-back two months. When the abundance of spiders, floral visitors and number of panicles in bloom were correlated to monthly precipitation, we found a positive significant correlation for spider abundance when the data were compared shifted-back three months, a significant negative correlation for floral visitors when the data were compared shifted-back two months, and a nonsignificant correlation for the number of panicles in bloom, although both (panicles and floral visitors) peaked in May.

Keywords: *Peucetia viridans*, *Cnidoscolus aconitifolius*, population structure, seasonality

Animals which are mobile during a period of their life actively select a site for nesting, feeding and reproduction. The latter may be influenced by parental habitat occupation, high density of competitors, or habitat availability at certain times of the year. The new site has to provide enough food, adequate nesting conditions, and protection against enemies and adverse weather conditions. Food resources are patchily distributed for most animals, regulating their feeding behavior, population dynamics, fitness and ultimately their evolution (Bronstein 1995). Thus, the fitness of an animal should be directly influenced by its ability to find a suitable habitat, which is based on an innate preference for certain high-

quality environmental characteristics (e.g., absence of enemies and availability of food and shelter). Object organization in space is used to locate such habitats (McCoy & Bell 1991). Environmental characteristics exert a strong influence on habitat selection in spiders (Uetz 1991). For example, spiders depend on the structure of the environment because: (1) they need attachment sites for their webs, and (2) their sensory organs are based on the recognition of tactile vibrations of the substrate (Rovner & Barth 1981; Uetz & Stratton 1982). Spider populations show certain associations between their structure and the heterogeneity and/or structural complexity of the plant community (Chew 1961; Riechert &

Reeder 1970). Certain spiders have highly specific associations with plants. Thus their abundance and richness depend directly on the availability of specific plant species. The association between spiders and plant community structure suggests stratification of species or habitat partitioning, which should decrease interspecific competition. Spiders select sites based on the level of protection against extreme temperatures and the destruction of webs and nests, maximizing foraging time on the web. Similarly, they use environmental elements as indicators of prey availability, e.g., plant flowering (Morse 1984; Pollard et al. 1995).

Our field observations in the Yucatán Peninsula, México, have shown a close association between the green lynx spider (*Peucetia viridans* Hentz, Oxyopidae) and *Cnidoscolus aconitifolius* (Mill.) I.M. Johnstone (Euphorbiaceae). However, the characteristics that determine this habitat selection are largely unknown. The purpose of this research was to describe quantitatively this spider-plant interaction, and to explain the physical and spatial characteristics of the habitat used by the spider. In particular, we addressed the following questions: (1) Which plant parts does the spider use more frequently? (2) Which plant characteristics determine the presence of the spider? (3) Are all the stages in the life cycle of the spider accomplished on *C. aconitifolius*? (4) How does the population of the spider vary through time? and (5) Is there synchrony between the flowering time of the plant and the life cycle of the spider?

METHODS

Study site and organisms.—Field work was conducted in a 13,000 m² grassland owned by Universidad Autónoma de Yucatán, located 15.5 km south of Mérida, Yucatán, México (20°58'N, 89°37'W, elevation 9 m), which is surrounded on three sides by grassland, and on one by tropical lowland dry forest (canopy height is ca. 15 m).

The genus *Cnidoscolus* is characterized by the presence of urticant compounds which contribute to plant defense against herbivores (Harborne & Turner 1984). *Cnidoscolus aconitifolius* has extrafloral nectaries which are visited by ants, flies, bees and wasps. The inflorescence is a panicle with feminine and hermaphroditic flowers (both flowers may be pre-

sent in one panicle) and has no specific pollinators (Carbajal-Rodríguez 1998). In the study site, *C. aconitifolius* is distributed in clumps of up to 12 individuals, but solitary individuals are common.

The green lynx spider (*Peucetia viridans*) is a cursorial hunting spider, foraging by day and night on a wide variety of prey, commonly living on wild flowers, grasses, low shrubs or weeds (Whitcomb & Eason 1967; Nyffeler et al. 1987a, b, 1992; Weems & Whitcomb 1977; Simon 1980; Van Niekerk & Dippenaar-Schoeman 1994; Whitcomb et al. 1966). It is the dominant polyphagous predatory arthropod in certain systems. Its diet includes several insect orders, spiders (including its own species), and at times it preys on individuals up to 2.5 times larger than itself (Nyffeler et al. 1988a, 1992). In Texas and Florida, *P. viridans* is frequently associated with *Croton capitatus* (Euphorbiaceae), and with related genera like *Gossypium* (Malvaceae) and *Helianthus* (Asteraceae), where it plays an important role as predator of noxious fauna (Randall 1982; Simpson 1995). *Peucetia viridans* is considered an annual univoltine species, with a reproductive season during the summer. Oviposition (25–600 eggs) is during the autumn, hatching and dispersal of juveniles by ballooning takes place during the winter; and growth of juveniles takes place in spring (Exline & Whitcomb 1965; Whitcomb & Eason 1965).

Sampling design and statistics.—Field observations were made between April and September of 1997 during the last 10 days of each month; a typical day started at 0800 h and finished at 1300 h. In the first visit we marked all *Cnidoscolus aconitifolius* individuals ($n = 183$) in the sampling site. For each plant we recorded height, cover (see below), number of panicles in anthesis, distance to the forested area, and their aggregation pattern (i.e., whether isolated or in a patch, see below). To estimate plant cover, we used the formula for an ellipse ($C = 0.25\pi D_1 D_2$, where D_1 and D_2 are two perpendicular diameters crossing the center of the plant) rather than a circle, because *C. aconitifolius* shrubs are quite irregular and fit better an oval shape. A plant was considered in a patch when its leaves overlapped with another individual and/or the distance between the base of their stems was no more than 40 cm; if these parameters were not

met the plant was considered as solitary. The distance to the forested area was considered important because (1) it is probably the source of young spiders colonizing *C. aconitifolius* individuals in the grassland, and (2) because environmental conditions are different closer to the forest (e.g., more shade and humidity, and less insolation).

On each visit we counted all *Peucetia viridans* individuals present per plant, and for each spider recorded: sex, activity (repose, foraging, feeding, care of offspring or egg sacs, courtship), location on the plant (on the stem, above or below a leaf, among new leaves, among the inflorescence, on a panicle), height above the ground, and size. To estimate size we used the width of the cephalothorax, which is relatively fixed per developing instars (nine instars for females, and eight for males) (Brady 1964; Killebrew & Ford 1985; Louda 1982; Randall 1978; Van Niekerk & Dippenaar-Schoeman 1994; Whitcomb et al. 1966). To accomplish the above, spiders were not removed from the plants. Instars were estimated using previously collected and measured individuals, which were organized by size in a cotton-stuffed vial and preserved in 70% alcohol. The vial was placed near a spider and size was established by comparison.

We estimated the abundance of floral visitors per month using five inflorescences on each of 10 isolated and 10 grouped individuals randomly selected. All visitors were counted when they made physical contact with the flowers at the time of peak activity (1200–1230 h). A three-way analysis of variance (SigmaStat 1995) was used to determine differences on the abundance of floral visitors among months and between isolated and grouped plants; the data was transformed by obtaining the square root of the value plus one (Zar 1996). We used a two-way analysis of variance (SigmaStat 1995) to determine if *P. viridans* exhibits (1) vertical stratification on the plant, (2) location preferences among instars and over time, (3) changes on activity intensity over time, and (4) comparison of spider abundance per plant grouping over time. A log-linear model was fitted with the GLIM-4 statistical system package (Francis et al. 1993) to test the hypothesis that spider presence is correlated to plant characteristics (number of panicles), and that synchrony exists between plant phenology, the life cycle of

the spider (abundance and instar-structure per month), and the precipitation pattern of the study site. Because we used “count data,” the goodness-of-fit was evaluated with a χ^2 test using the *G* statistic and a Poisson error distribution. With Poisson errors, the change in variance can be compared directly with χ^2 tables to assess its significance (Crawley 1993).

In order to estimate the synchrony between plant phenology and the life cycle of the spider, we compared the number of blooming panicles of *Cnidioscolus* and the number of floral visitors to the abundance of *Peucetia* per month. As organisms usually need time to respond to changes in their environment (e.g., Ogata et al. 1996), these correlations (Pearson) were computed following a time lag scheme, which consisted in taking the resultant spider abundances for a specific month and correlating them with the blooming panicles and/or floral visitors abundances of the preceding months. Correlations were computed at one, two and three months time lag.

RESULTS

Population parameters.—Highest spider density was recorded in August (total 118, adults 77), and lowest in May (total 7, adults 2) (Table 1). Spider density was significantly higher in isolated plants and lower in plants in a patch ($F = 9.849$; $P = 0.026$). Sex ratio ($\text{♀}:\text{♂}$) varied from 1:1.5 in April, to 1:1 in May, and to 1:0.1 in September (Table 1). The dominant instar (both sexes) changed during the study. For example, instar IV in April, instar V in May, instars VI and IX in June, instars VII and IX in July, instars VIII (mature males) and IX (mature females) in August, with the onset of the reproductive season and the appearance of instar I; while in September the number of mature males (instar VIII) decreased and instars I, II, and III increased (Fig. 1).

Activity.—Throughout the study more spiders were in ‘repose’ than in any other activity. Foraging and feeding were more intense between July and September when their prey, flower visitors, were more abundant. The care of egg sacs and offspring also follows a similar pattern (Fig. 2).

Habitat selection.—The number of spiders on plants of *C. aconitifolius* varied spatially and temporally due to the combined effects of distance of the individual plant to the nearby

Table 1.—Abundance and sex ratio per month of *Peucetia viridans* living on *Cnidoscolus aconitifolius*.

Month	Number of spiders			Spider sex ratio ♀ : ♂	Number of plants sampled	Spider density per plant			Number of spiders per plant aggregation	
	Imma- ture	Adult	Total			Immature	Adult	Total	Isolated	Grouped
April	13	5	18	1:1.5	95	0.14	0.05	0.19	16	2
May	5	2	7	1:1	181	0.03	0.01	0.04	5	2
June	20	13	33	1:0.6	178	0.11	0.07	0.19	19	14
July	34	39	73	1:0.4	183	0.19	0.21	0.40	48	25
August	41	77	118	1:0.6	183	0.22	0.42	0.64	61	56
September	31	34	65	1:0.1	183	0.17	0.19	0.36	36	26

forest, monthly precipitation, plant height, and number of panicles in anthesis. The generalized linear model fitted explained 9.59% of the variation (Table 2). Spider abundance was significantly and positively associated with plant height ($\chi^2 = 23.07$, $df = 1$; $P < 0.01$; 1.98% of total variance). On the other hand, spider abundance was significantly and negatively correlated to distance to the nearby forest ($\chi^2 = -43.53$, $df = 1$; $P < 0.01$; 3.73% of the total variance), monthly precipitation ($\chi^2 = -23.35$, $df = 1$; $P < 0.01$; 2.17% of total variance), and the number of panicles in bloom ($\chi^2 = -9.72$, $df = 1$; $P < 0.01$; 0.83% of total variance). The interaction between distance to nearby forest and precipitation was also positively correlated with spider abundance ($\chi^2 = 6.28$, $df = 1$; $P < 0.01$; 0.54% of total variance); at the onset of the rainy season spiders were found near the forest, and as precipitation increased, the distance to the forest at which spiders were found also increased. We also found a positive significant correlation between the interaction of precipitation \times number of panicles in bloom, and spider abundance ($\chi^2 = 3.98$, $df = 1$; $P < 0.01$; 0.34% of total variance).

Forty-eight percent of the spiders were found living on plants with a range of 20–30 panicles in anthesis; which only represents 2% of the *C. aconitifolius* population. Most of the spiders were found either below or above leaves. We did not find significant differences among spider location sites on the plant, except for below and above leaves compared with those less used sites (i.e., fruits and panicles, $F = 4.613$; $P < 0.01$). Likewise, most developmental stadia did not show structure preferences. Instar IX (adult females) differed

significantly from the other instars ($F = 2.166$; $P = 0.044$) because quite frequently they were found living below the leaves. There were no significant differences in the distribution of most instars respective to plant height because most spiders were found between 60–80 cm. Again, only the location of instar IX was statistically different from the rest ($F = 7.519$; $P < 0.001$), usually nesting at heights between 1–2 m.

Synchrony between phenologies.—The number of flower visitors, the number of panicles in anthesis, the number of spiders, and the precipitation data per month are presented in Fig. 3. Grouped plants had significantly more floral visitors than isolated plants, and peak visitation was in July; we did not find differences in number of visitors among plant individuals either isolated or in groups (Table 3). There is a clear displacement in time among the peaks of blooming panicles (May), floral visitors (July), spiders (August), and precipitation (May and September). Positive significant correlations were found between the number of spiders and the abundance of floral visitors when the data was compared with one month time lag ($r = 0.891$, Pearson (r_s)_{0.05(2),6} = 0.755, $P = 0.042$), and between the number of spiders and the number of panicles in bloom when the data was compared with two months time lag ($r = 0.93$, Pearson (r_s)_{0.05(2),6} = 0.811, $P < 0.05$). When the abundance of spiders, floral visitors and number of panicles in bloom were correlated to monthly precipitation, we found a positive significant correlation for spider abundance when the data was compared with three months time lag ($r = 0.949$, Pearson (r_s)_{0.05(2),6} = 0.77, $P < 0.05$), a negative significant correlation for

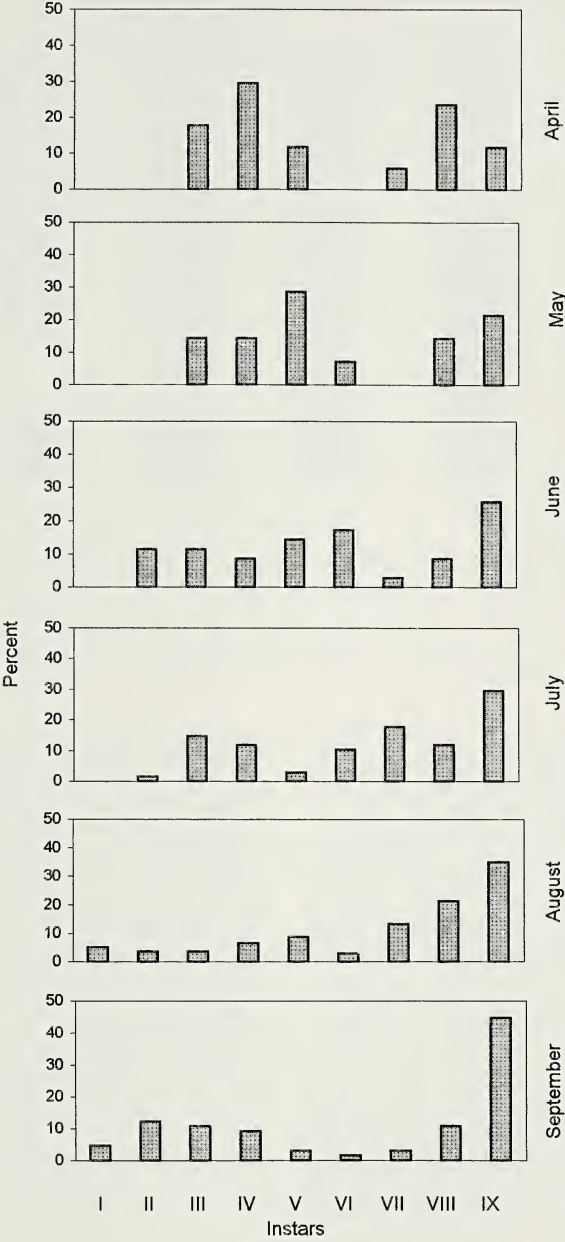


Figure 1.—Instar distribution of the population of *Peucetia viridans* through the year in Mérida, Yucatán, México. Instars I to VIII correspond to males and females, instar IX only adult females (see text, sampling design).

floral visitors when the data was compared with two months time lag ($r = -0.775$, Pearson (r_s)_{0.05(2),6} = 0.77, $P < 0.05$), and a non-significant correlation for the number of panicles in bloom ($r = 0.042$, Pearson (r_s)_{0.05(2),6} = 0.77, $P > 0.05$), although both peaked in May.

DISCUSSION

The life cycle of *Peucetia viridans* has been reported (Florida, Texas and Baja California) to start with the mating season in July, eggs are laid in September, hatching and dispersal between November and early January, and growth from January to June, when males and

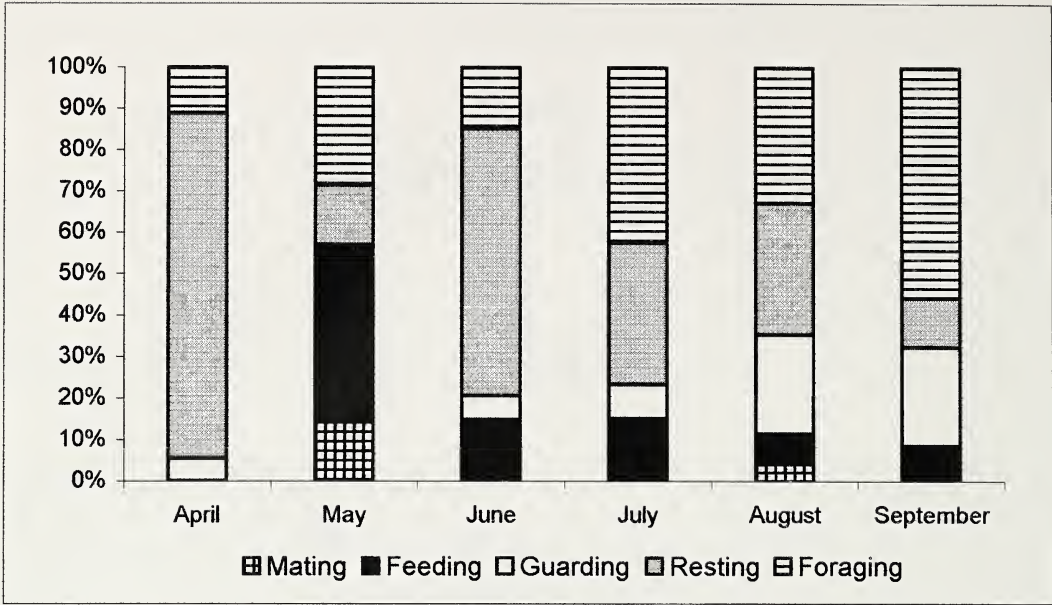


Figure 2.—Frequency of the different activities recorded for *Peucetia viridans* inhabiting *Cnidoscopus aconitifolius* in Mérida, Yucatán, México.

females reach their mature state (Brady 1964; Whitcomb & Eason 1966; Louda 1982; Van Niekerk & Dippenaar-Schoeman 1994). In Yucatán the cycle is similar, although displaced two months due to differences in the climatic patterns between our study site and the areas where the latter studies were accomplished. In Yucatán, the abundance of *P. viridans* increases when precipitation increases and temperature decreases, courtship and mating start in May, and mating peaks between June and August. One female was found guarding an egg sac in April, none were recorded in May, while this activity increased through August (26 females guarding egg sacs and progeny); finally, hatching and dispersal

occurred between August and September. Feeding behavior increased in May which coincides with the pre-mating season, pre-adult maturation and growth of juveniles. Foraging behavior was well represented throughout, except for April and June. In summary, despite localities and changes in weather patterns, it seems that the phenology of the spider closely follows the changes in the physical environment of each site. Louda (1982) found that *P. viridans* was associated with the larger individuals of *Haplopappus venetus* (Asteraceae) rather than on younger plants or on those with taller inflorescences. Our population of *C. aconitifolius* differed in the number of panicles in bloom

Table 2.—Summary of results from the generalized linear models fitted to the data on plant physical characteristics, distribution pattern, and number of spiders present.

Source of variation	χ^2	df	% of variation	P
Distance to forest (A)	-43.53	1	3.73	<0.01
Precipitation per month (B)	-25.35	1	2.17	<0.01
Plant height	23.07	1	1.98	<0.01
Panicles in anthesis (C)	-9.72	1	0.83	<0.01
A * B	6.28	1	0.54	<0.01
B * C	3.98	1	0.34	<0.01
Error	1051.87	1	90.38	
Total	1163.8		100	

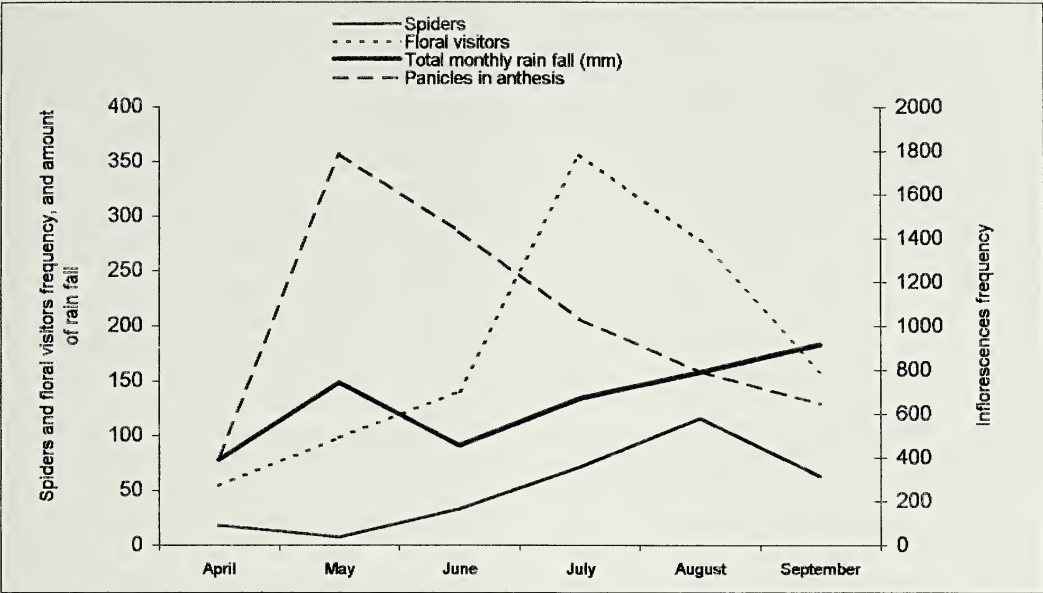


Figure 3.—Abundance of *Peucetia viridans*, number of panicles in bloom of *Cnidoscolus aconitifolius*, floral visitors and precipitation per month at the study site.

per plant, and more spiders were found on taller plants, with more panicles in bloom, more cover, and closer to the nearby forest patch. Sixty-five percent of the plants had between 0–5 panicles in bloom, but only 2% of the spiders were found on these plants, whereas 48% of the spiders inhabited plants with 20–30 panicles in bloom. We suggest that this pattern could be the result of the dispersal behavior (ballooning) of the spiderlings of *P. viridans*, who may take refuge in the nearby forest patch during the first months of their development, and then move back to *C. aconitifolius* individuals. Morse (1993) has proved that spiderlings may balloon more than once, increasing their probability of placement on a satisfactory hunting site. *Peucetia viridans* could be selecting larger plants (i.e., with more panicles in bloom) which will attract more floral visitors and where the spider will gain protection from the extended plant cover;

while they may select isolated plants in order to avoid or decrease competition for space. Crab spiders rely heavily on cues from the environment, such as the quantity of nectar in a flower, or the number of flowers present (Morse & Fritz 1982). We suggest that *P. viridans*, guided by color recognition and/or the amount of floral nectar, chooses plants based on the number of panicles in bloom, which increases the number of visitors, and thus spider survivorship. Morse (1991) demonstrated that *Misumena vatia* actively chooses its territory, moving from poor to high quality inflorescences. Crab spiders do not seem to respond to unopened flowers or to the number of nectar-secreting flowers, instead, they direct their response to the number of insects attracted to plants (Morse 1988). Our results suggest that *P. viridans* is selecting plants based mainly on the number of panicles in bloom and plant height.

Table 3.—Summary of the results of the three-way ANOVA comparing the abundance of floral visitors per month, visiting isolated and grouped plants.

Source of variation	df	MS	F	P
Date (month)	5	16.43	11.60	< 0.001
Plants (grouped/isolated)	1	99.81	70.51	< 0.001
Differences among plants	4	0.940	0.664	= 0.624

We expected to find an association between spider age and their vertical distribution on the plant, since adult females were found living and foraging on taller branches and inflorescences, and juveniles (3rd and 4th instars) on lower locations. However, with the exception of adult females who sought high places to lay their egg sacs, the rest of the developmental stages did not show a preferred nesting or foraging height. We did not find either any preference for location on the plant among instars. Most of the spiders were found above (34%) or below (37%) leaves, and only 15% of the spiders were found on inflorescences; but there was no preference by instar or time of year. Morse (1993) found that crab spiders choose specific leaf areas to build their nests, particularly close to favorable spiderling hunting sites. Gravid females of *P. viridans* choose the more shaded plants nearest to the forest patch, decreasing the probability of spiderling desiccation and increasing the potential food resources (more panicles in bloom). Crab spiders are very efficient in choosing the umbel with the largest number of white flowers, and the fact that their presence resembled the frequency with which insects visited umbels, rather than the number of flowers visited on these umbels, suggests that the mere appearance of an insect, however fleeting, provides the spider with the single largest amount of information required to make a choice (Morse & Fritz 1982). Thus the frequency of spider attack on their prey should provide us with useful information on site quality (Morse & Fritz 1982).

Louda (1982) found in Baja California that flowering was correlated with the relative abundance of spiders and floral visitors. In Yucatán the flowering peak occurred in May, the peak of flower visitors in June, and the peak of spider abundance in August. However, the resulting significant correlations (either with one, two or three months of time lag) among the above variables, suggest that organisms need time to respond to changes in their environment. The latter could also be an escape strategy of the plant, since blooming panicles are available to pollinators when the abundance of *P. viridans* is low.

Not all individuals of *C. aconitifolius* were inhabited by *P. viridans*. Interestingly, these were visited by geometer caterpillars which heavily damage leaves (Parra-Tabla & Car-

bajal-Rodríguez, unpubl. data). Freitas & Oliveira (1996) have demonstrated that butterflies visually recognize potential egg predators, such as ants, and actively choose sites that are better for egg-laying, thereby reducing the risk of death of their offspring. It is quite possible that the geometer moths ovipositing on *C. aconitifolius* recognize *P. viridans* and thus only oviposit on those plants without spiders. Even though spiders prey heavily on the plant's pollinators, they may also impede oviposition by the moth on the plant and thereby reduce potential leaf damage, benefiting the plant (see also Louda 1982).

Finally, our results suggest that *Peucetia viridans* uses high-quality portions of its habitat, choosing those plants offering better sources of food, shelter, and favorable environmental conditions. The study of tritrophic-level interactions (e.g., plant-herbivores and/or pollinators-predators, such as spiders) should be pursued because they may yield more information on how different clustering of relationships between species affect the ecology and evolution of interactions (Price et al. 1980; Thompson 1994).

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FOOD CONSUMPTION RATES AND COMPETITION IN A COMMUNALLY FEEDING SOCIAL SPIDER, *STEGODYPHUS DUMICOLA* (ERESIDAE)

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ABSTRACT. A major factor which affects an animal's consumption rate is competition for food items. Competition usually results in a drop in consumption rate; however, this may be counteracted if the animals can exploit the foraging efforts of others, as could occur in social spiders when feeding on the same prey item. Spiders digest prey extra-orally and might utilize the enzymes or digesta produced by other individuals feeding from the same prey item. We investigated prey consumption in the social spider *Stegodyphus dumicola* to determine if the rate of consumption of individual spiders changed in the presence of competitors. We found that when one spider fed on small prey, food consumption rate decreased with feeding duration. When the prey was larger in relation to the spider there was an initial delay in consumption. There was no apparent advantage for a second spider to feed on a prey item already being consumed: the second spider fed for less time and gained less mass. These results indicate that social spiders compete during the process of food ingestion and the presence of another spider reduces the value of the prey item to a subsequent forager.

Keywords: Competition, sociality, foraging

Foraging theory indicates that the rate at which food is consumed at a patch strongly influences the residual value of that patch to an animal (Krebs et al. 1974; Charnov 1976; Iwasa et al. 1981). Competition among conspecifics can reduce consumption rate by reducing the residual amount of food in a patch available to the forager, or by reducing the amount of time available for foraging owing to time lost in direct physical confrontation (Sasvari 1992).

In group-feeding social species, competition during foraging and feeding is expected to be less extreme than in solitary species. Social spiders are those that live in communal webs in which there are no individually defended territories (D'Andrea 1987; Avilés 1997; Whitehouse & Jackson 1998). Social spiders cooperate in capturing prey which is then consumed by a group of individuals. By cooperating, they can handle larger prey than most similar-size solitary species (Nentwig 1985; Rypstra & Tirey 1991; Rypstra 1993; Pasquet & Krafft 1992).

Spiders feed using extra-oral digestion in which they pump enzymes into the body of the prey and then ingest the emulsified contents (Collatz 1987; Cohen 1995). Extra-oral digestion affects the rate at which food can be consumed by such a predator during a feeding bout. As enzymes need time to digest prey, the predator may not ingest much food in the initial stages of feeding, but it can consume food at a fast rate later on, once the prey is digested. In social spiders many individuals can feed on the same prey, which may mean they have access to each other's enzymes. This could result in spiders exploiting enzymes and digesta of other individuals (Ward & Enders 1985; Whitehouse & Lubin 1999). In this situation, the presence of conspecifics feeding concurrently on a food item may actually increase the value of the food item and increase the rate of consumption for the "exploiting" spider.

The timing of feeding by an individual within a group foraging event could influence its rate of prey consumption. If the prey is initially digested slowly and then later digested quickly, it may be advantageous to feed from the prey later in the foraging event, after

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other spiders have injected enzymes and digestion has begun. Alternatively, if the prey is digested quickly and consumption is initially fast but quickly drops off, then the first to feed will gain the most and it may be advantageous to lead the attack on the prey in order to secure the best feeding position. Attacking first, though, is potentially hazardous. The attacker must subdue the prey, possibly depleting its poison reserves and putting itself at risk. Thus, the rate of prey consumption can influence both the attack and the feeding strategies of group-feeding spiders. Factors which have been shown to affect consumption rate in extra-orally digesting predators include the size of the prey relative to the predator (Cohen & Tang 1997; Erickson & Morse 1997), the type of prey involved (Leborgne et al. 1991), and the size of the feeding group (Ward & Enders 1985).

We studied the feeding behavior of the social spider *Stegodyphus dumicola* (Eresidae) to determine the influence of the presence of a conspecific on the trajectory of prey consumption. *Stegodyphus dumicola* occurs in southern Africa in colonies of up to several hundred individuals. The spiders cooperate in nest construction, care of young and prey capture, and readily feed together in large groups (Seibt & Wickler 1988; Wickler & Seibt 1993). We examined the consumption rate of "groups" consisting of only two animals feeding on small grasshoppers of half to two-thirds their body size and compared consumption rates of members of a pair and of solitary individuals. While a group size of two individuals is unusual, such groups do occur in nature (Henschel 1991/1992); and even in larger nests, small prey items are often attacked by only a few individuals (Lubin pers. obs.).

METHODS

Colonies of *S. dumicola* containing juveniles were collected in Namibia in January 1996 and housed in Sede Boker, Israel, in a climate-controlled room at 27 °C. and a photoperiod similar to outside conditions. Experiments were conducted from July 1996 to March 1997, and all spiders used in the experiments were derived from the same colony. The spiders were all juvenile females weighing about 40 mg, or about two-thirds adult

size. Voucher specimens are deposited at the Mitrani Department for Desert Ecology.

Food consumption pattern of single spiders.—Consumption rates were determined for spiders feeding alone in two tests. Because the tests were separated by a few weeks, spiders in the second test were larger than those in the first. In the first test, 51 individuals of similar body size were drawn from the colony and put in individual plastic containers (a cylinder 30 cm long, diameter 12 cm) with supports for web building, where they were given seven days to acclimate. After a week, each spider was weighed on an analytical balance to the nearest 0.1 mg, and then fed one grasshopper nymph. We recorded the time until the spider attacked the prey, and the length of time the spider fed (excluding pauses in feeding). Different individuals were allowed to feed for predetermined durations (15, 30, 60, 90, 120, 180, and 240 min) after which feeding was stopped and each spider was reweighed.

In the second test, conducted concurrently with the test of pairs of spiders (see below), 23 individuals were allowed to feed for different durations, as in the first test. There was a small, but significant difference in body sizes of spiders between the two tests ($t = -4.6$, $df = 72$, $P < 0.001$; average body mass in the first test: 42.15 ± 5.7 mg, second test: 48.6 ± 5.3 mg). The prey mass was increased in the second test ($t = -11.6$, $df = 72$, $P < 0.001$; average prey mass in the first test: 19.3 ± 3.6 mg, second test: 29.5 ± 3.2 mg). The ratio of prey mass to spider mass was higher in the second test (0.61 ± 0.05) than in the first (0.465 ± 0.1 ; arcsin transformed ratios, $t = -6.85$, $df = 72$, $P < 0.001$).

Food consumption of pairs.—Twenty-one pairs of spiders were matched for size (body mass: 46.7 ± 6.3 mg; average mass difference between pairs = 3.5 mg, range 0–14.6 mg). To distinguish between pair members, bee numbers (numbers designed for use in apiaries) were glued to the abdomen with transparent nail polish. The pairs were placed in plastic containers and left for seven days to acclimate. Before the experiment each spider was weighed, and each pair was given one grasshopper nymph. We recorded the time until the first spider attacked the prey, and the duration of feeding (excluding pauses in feeding). Once the first spider had fed for a pre-

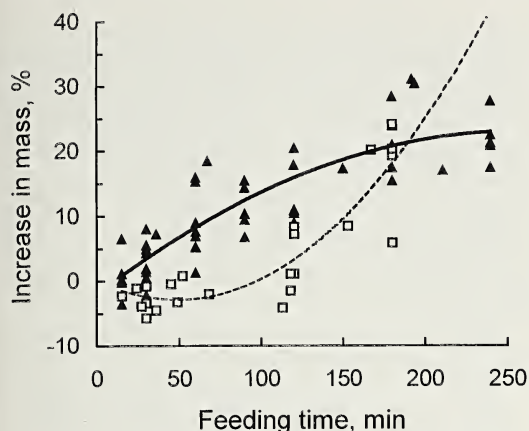


Figure 1.—Relative consumption rates (% increase in body mass) of spiders feeding alone: a comparison of two ratios of prey/spider mass. Filled triangles (▲), heavy line: low ratio = 0.465 ± 0.1 ; open squares (□), thin line: high ratio = 0.62 ± 0.07 . The polynomial regression of the low-ratio curve is: $y = -x^2 + 0.19x - 2.03$, $R^2 = 0.74$; the regression of the high-ratio curve is: $y = x^2 - 12x + 0.09$, $R^2 = 0.78$ (percentages were arcsine transformed for the regressions).

determined length of time (either 15, 30, 60, 90, 180, or 240 min) the experiment was stopped. If the second individual had begun to feed, we recorded the time it began to feed and the duration of feeding.

RESULTS

Food consumption pattern of spiders feeding alone.—The rate of food consumption by spiders feeding alone was examined in the two different tests. When spiders fed in the absence of conspecifics (first test), their body mass increased with the time spent feeding ($F_{1,23} = 39.8$; $P < 0.001$). However, there was a significant difference in mass gain between the first and second tests (ANCOVA: final body mass with initial mass as covariate, $F_{1,71} = 7.94$, $P = 0.006$; Fig. 1) which was caused by differences in the trajectories of mass increase experienced by the two groups. In the first test, the relative change in body mass was initially linear and began to asymptote after two hours. In the second test, the coefficient changed sign, and the spiders began to show an increase in body mass only after an hour of feeding. The difference between the two tests is explained in part by the different prey mass/spider mass ratios. In a general linear model, both prey mass and

feeding time were significant ($P < 0.001$, $n = 74$, with initial spider mass as covariate), together explaining 87.4% of the variance in final spider body mass for both tests.

Food consumption of spiders in pairs.—When all 21 pairs of spiders were considered, the trajectories of prey consumption of first and second spiders did not differ (ANCOVA, $P > 0.1$; combined regression, $y = 0.002x + 0.055$, Fig. 2). However, in 12 instances (57.1%), only a single spider of the pair fed. To establish whether one spider in a pair fed alone significantly more often than both spiders together, we needed to take into account the fact that we stopped spiders at different times after they started to feed. In the above 21 pairs, the maximum time taken for the first spider to attack the prey was 170 minutes. If we assume that the second spider responded to the prey in the same manner as the first spider, it should also have a maximum delay of 170 minutes before beginning to feed. Consequently, we removed the eight tests in which the experiment was stopped before it had run for 170 minutes. Of the remaining 13 tests, although the first spider fed in all of them, the second spider fed in only six instances (comparison of first and second spiders, Fisher's exact test, $P = 0.005$).

There was a short but variable delay between the attack of the first and second spider (median = 16 min, range = 8–164 min, $n = 9$). The first spider always fed longer than the second spider (Wilcoxon signed ranks test, $z = -2.67$, $P = 0.008$, $n = 9$), and there was a trend for the first spider to gain more mass than the second (Wilcoxon signed ranks test, $z = -1.7$, $P = 0.086$, $n = 9$). We tested for differences in the consumption rates of the first and second spiders that fed together by comparing the regressions of final body mass on net feeding time, with initial body mass as covariate. The consumption rate of the first spider was greater than that of the second spider to feed (ANCOVA, $F_{1,15} = 4.244$, $P = 0.057$).

Mass loss.—Some spiders lost mass during the feeding trials. The mass lost by the spiders was always larger than the measurement error due to weighing inaccuracy, which was calculated at 0.08 mg. In the first test with single spiders, four spiders (7.8%, $n = 51$) lost mass (median = -0.6 mg, range = -0.1 to -1.3 mg); all had fed for 15–30 min. Twelve spi-

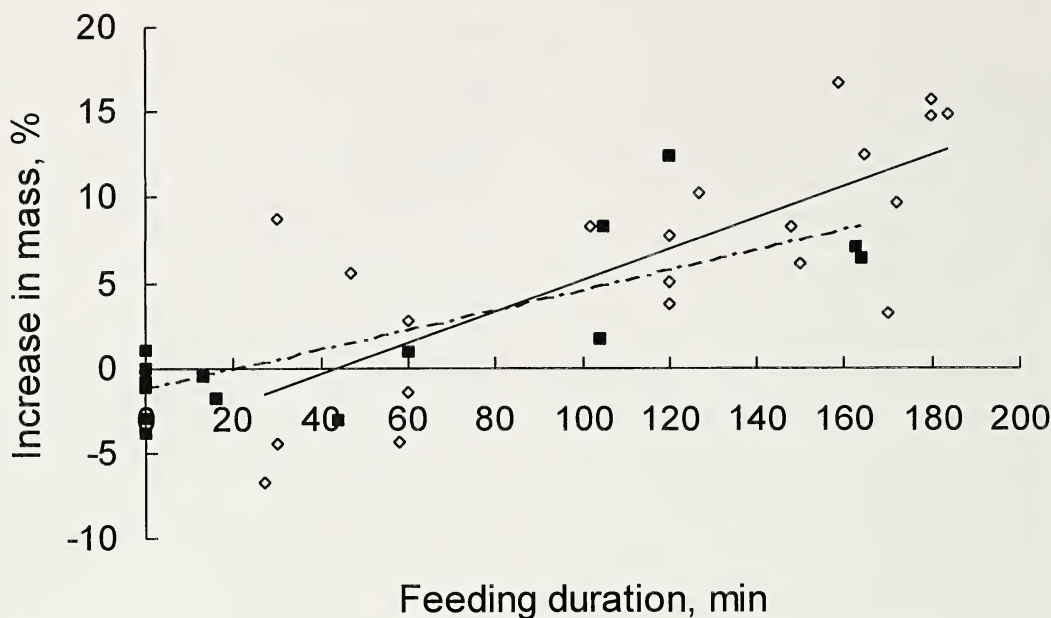


Figure 2.—Relative consumption rates of spiders feeding in pairs: percent increase in body mass against net feeding time of each spider. First spider to begin feeding: open diamonds (\diamond), solid line; second spider: closed squares (\blacksquare), dashed line. The regression equations are: first spider, $y = 0.092x - 3.98$, $R^2 = 0.58$; second spider, $y = x^2 + 0.06x - 1.13$, $R^2 = 0.655$ (arcsin transformed percentages).

ders lost mass in the second test (median = -1.25 mg, range = -0.2 to -3.0 mg), with feeding durations ranging from 15–118 min (median = 33 min). The feeding duration of spiders that lost mass was significantly shorter than of those that gained mass (median = 120 min, range 52–180 min; Mann-Whitney $U = 6.5$, $P < 0.001$, $n = 23$).

In spiders that fed in pairs, a decrease in body mass occurred in three first and nine second spiders. As the sample sizes were small, we used bootstrapping (Simon 1995) to determine the probability that the observed difference between the median mass loss in the two groups occurred by chance alone. There was no difference in mass loss between second spiders that fed ($n = 3$) and second spiders that did not feed ($n = 6$, $P = 0.21$). However, first spiders that fed and lost mass ($n = 4$) tended to lose more than second spiders that fed and lost mass ($n = 3$, $P = 0.087$) and more than the single spiders of the concurrent second test ($n = 12$, $P = 0.078$).

DISCUSSION

When solitary spiders fed on small prey items, their body mass increased with feeding time. In the first test with single spiders, using

relatively small prey (prey/spider mass = 0.465), the gain followed a typical curve of diminishing returns, similar to that shown by the spider *Zygiella x-notata* (Araneidae) feeding on cricket nymphs (prey/spider mass = 0.1–0.3; Leborgne et al. 1991). Thus, small prey items, less than half the mass of the spider, are rapidly depleted. Another spider attempting to feed on the same prey item would gain no advantage by waiting, and would obtain more food by joining early in the feeding bout.

With larger prey (prey/spider mass = 0.6), there was a delay in the spider's consumption, resulting in a feeding trajectory with the opposite sign to that above (Fig. 1). The lag before the initial increase in food intake might be due to the time necessary for enzymes to take effect in digesting the larger meal. The delay was more pronounced when spiders fed alone than when they fed in pairs. This suggests that the presence of conspecifics caused spiders to increase their consumption rate.

During the initial period on the prey, when venom and enzymes are presumably being pumped into the prey, spiders may even lose mass. Although sample sizes were small, mass

loss was greater in first spiders than in second spiders or spiders feeding alone (comparing only those individuals that lost mass). Thus, with large prey it may be advantageous for a second spider to join later and capitalize on enzymes injected by the first spider (Ward & Enders 1985). In tests with pairs of spiders, however, we found that the second spider tended to join early in the feeding bout. In spite of possible advantages of such "enzyme piracy" (Whitehouse & Lubin 1999), second spiders fed for less time than the first spiders and had lower consumption rates.

The advantage shown for the first spider to feed agrees with other studies of group feeding in social spiders. Willey & Jackson (1993) found that in *Stegodyphus sarasinorum*, when tested in groups of 10 individuals, spiders that attacked first fed for longer duration than those that arrived later. In *Stegodyphus mimosarum* (Ward & Enders 1985), the first spider of a pair to attack did not feed longer than its partner, but fed more frequently from the thorax and head of the prey, body parts which yield the highest reward (Robinson 1969), while its partner showed no feeding site preference. Likewise, in a group of five individuals of *S. dumicola* matched for size, the first spider that attacked the prey tended to obtain more food, but did not feed for longer (Whitehouse & Lubin 1999). In the latter study the individuals that gained the most mass were those that fed longest during the middle part of a foraging bout, although they also tended to initiate the attack (Whitehouse & Lubin 1999).

Competition over prey occurs in cooperative group-living spiders (Ward & Enders 1985, Whitehouse & Lubin 1999), but it is apparent mainly in differences in rates of food consumption. In the social *Stegodyphus*, there is little evidence of active competition in the form of aggressive interactions over prey. In this study, we found that when the prey item is smaller than the spider, often only a single spider will attack and feed, and when two individuals do feed together, the second obtains less food from the prey. The results of this study suggest that "piracy" of enzymes or digesta may occur, and that spiders may adjust the timing of feeding and their consumption rate to compensate for losses due to other individuals. These considerations as well as differences in possible trajectories of food con-

sumption, e.g., in relation to the relative size of prey and spider, may influence the decisions to join an individual feeding on a prey item. Further studies of the dynamics of group feeding and the physiology of food ingestion are needed to understand the costs and benefits of group feeding in social spiders.

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PREDATOR AVOIDANCE ON THE WATER SURFACE? KINEMATICS AND EFFICACY OF VERTICAL JUMPING BY *DOLOMEDES* (ARANEAE, PISAURIDAE)

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ABSTRACT. Vertical jumps of fishing spiders (*Dolomedes* sp.) from the water surface have been presumed to be evasive behaviors directed against predatory fish. We used high-speed videography to analyze the jumps of fishing spiders and then constructed a numerical model to assess the effectiveness of these jumps in evading predatory strikes by trout. Jump height (mean = 3.7 cm) and duration (mean = 0.17 sec) were similar across spider masses (0.05–0.66 g) but latency to jump increased significantly with mass. To accomplish jumps of similar height, more massive spiders had to generate more force during the propulsive phase of the jump than did smaller spiders; and the contribution of fluid drag to the total force used in jumping was substantially greater for large spiders than for smaller ones. Our model juxtaposing the jumps of spiders and the attacks of trout revealed that jump heights and durations were inadequate: only the most lethargic strikes by trout could be successfully evaded by jumping vertically from the water surface.

Keywords: Hydrodynamics, aquatic locomotion, predation, spider, *Dolomedes*

Fishing spiders (*Dolomedes* sp.; Araneae, Pisauridae), noted for their locomotion on the water surface (e.g., Barnes & Barth 1991; Shultz 1987), are adept at predation both on land and on the surface of ponds and slowly flowing streams (Gorb & Barth 1994). While on the water surface, they can also become prey, captured not only by animals that detect them from above (e.g., frogs, birds) but also by submerged predators (fish). One of the best studied of the fishing spiders, *D. triton* (Walckenaer 1837), has two well-known responses to danger from above: it either disappears under the water surface by climbing downward on submerged vegetation (McAlister 1959; pers. obs.) or it rapidly gallops away across the water surface (Suter & Wildman 1999; Gorb & Barth 1994). We and others (G. Miller, pers. comm.; Suter 1999) have observed that, when startled by sudden water-borne vibrations while at rest on the water surface, these spiders jump vertically and then either gallop away or return to rest. Our working assumption is that the jump functions to decrease the probability of capture by fish. Is this a reasonable assumption?

At first glance, a vertical jump from the water surface would seem to be ineffective as evasive behavior because the spider would

land exactly where it started, presumably exactly where the attacking fish had aimed (Fig. 1). But fish (e.g., trout, *Oncorhynchus* spp.) accelerate rapidly when lunging at prey (Domenici & Blake 1997), and rarely do so from directly below their intended victims. Thus an attacking fish usually has a non-vertical trajectory, and a vertical jump by a spider would be effectively evasive if it began in time, were high enough, and were of long enough duration.

The height and duration of a jump, closely linked to each other by the physics of gravitation, depend upon the acceleration the spider can impart to itself by pushing down against the substrate (water, in this case). In earlier studies (Suter et al. 1997; Suter 1999; Suter & Wildman 1999) our laboratory established that the locomotion of fishing spiders on the water surface is based on fluid drag: during horizontal rowing, for example, the dimples in the water surface (caused by the downward push of the spider's hydrophobic legs) move backward as the spider strokes, encounter resistance due to drag, and thereby impart a forward acceleration to the spider. In the current study, we looked closely at the forces involved in jumping because, as with rowing, the forces generated by the interactions of spi-

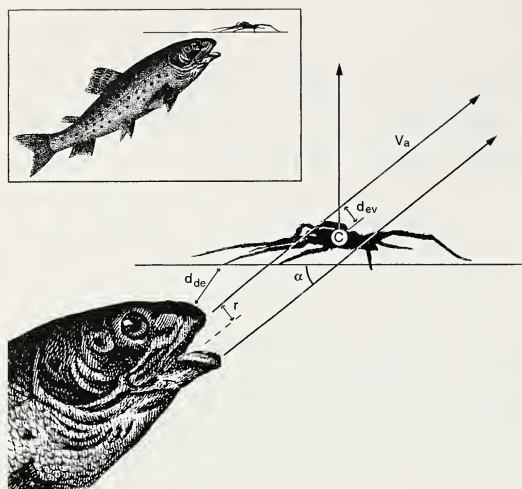


Figure 1.—Diagram of the evasion model. See text for explanation.

der motions and water ultimately govern the qualities of a jump.

METHODS

Spiders.—*Dolomedes triton* are found throughout temperate North America where they inhabit the edges of ponds and slowly flowing streams (Gertsch 1979). The subjects for this study were collected from small ponds in Mississippi and were held in our laboratory under conditions described elsewhere (Suter et al. 1997). Voucher specimens are deposited with the Mississippi Entomological Museum at Mississippi State University. All observations and experiments were conducted at laboratory temperatures between 20–23 °C during local daylight hours.

Kinematics of jumping.—The arena for our studies was a 38 liter aquarium filled to a depth of approximately 4 cm with distilled water. In a trial, we placed the test spider in the arena and used a slender glass rod or gentle puffs of air to maneuver the animal into the center of the arena. At that position its body was at the point of sharpest focus of either a high-speed video camera (Kodak model EktaPro EM-1000) or a 35 mm single lens reflex still camera (Nikon N70). We elicited a jump by sharply hitting the table that supported the aquarium at a distance approximately 2 cm from one corner of the aquarium (approximately 0.3 m from the spider).

The images from the high-speed video were collected at 1000 images per second and

stored in S-VHS format (Sony model 9500 MDR). We analyzed the spider's motion in the vertical plane by displaying each digitally-paused video frame on top of a computer-generated x-y cursor grid (NIH Image software, version 1.55 f) by means of a video scan converter (Digital Vision, Inc., model TelevEyes/Pro, connected to an Apple Corporation computer, Power Macintosh 7100/80AV). We then manually digitized the coordinates of the body's approximate center of mass (midway between the top and the bottom of the posterior margin of the cephalothorax) every 5 ms for the duration of a jump, and used the coordinates to calculate the displacement of the spider through time; velocity was calculated for each 5 ms interval. We selected several trials on which we used the same techniques to digitize the locations of the tips of the legs nearest to the camera.

To measure latency, the time between delivery of the stimulus and the first jumping movements, we placed a 2 × 3 cm mirror in the frame of view of the camera and angled it so that the high-speed video would show both the production of the stimulus and the motion of the spider. The vibrations caused by the stimulus could have reached the spider via transmission through about 0.28 m of water (assuming it propagated from the corner of the aquarium) or through only 4 cm of water (assuming it propagated first along the glass base of the aquarium and then vertically through the water directly below the spider. In either case, the vibratory stimulus would have reached the spider in < 0.2 ms (given a transmission velocity of 1497 m/s in distilled water; Weast 1985).

To make still photographs (35mm) of spiders during jumps, we used a percussion sensor and an electronic short-interval timer (LPA Design, LPA Time Machine) to trigger an electronic flash (Vivitar, 285HV) after a known post-stimulus delay.

Calculation of vertical forces.—We used two methods to calculate the vertical forces produced by spiders during jumping. First (the "acceleration method"), we calculated average force production by applying Newton's second law ($F = ma$) to our data on spider mass and acceleration (above). Second (the "leg-motion method"), analyses of the kinematics of jumping gave us information about the dynamics of the sub-surface portion of the

legs. We assumed that, although the sub-surface portion of a leg was not entirely surrounded by water, its motion through the water created a drag force identical to that created by a fully submerged leg segment of the same length and moving at the same average velocity. This is a plausible assumption for two reasons. First, the drag on a submerged cylinder is proportional to the frontal surface area (Denny 1993). And second, our earlier work (Suter & Wildman 1999) showed that Denny's equation for drag on a submerged cylinder, which incorporates both drag coefficients and Reynolds numbers (equation 4.29 in Denny 1993), fit the force data for the legs of spiders galloping across the water. We used Denny's equation to calculate the total thrust force exerted by that leg segment in a direction perpendicular to the leg's long axis, and used trigonometry to resolve that vector into its horizontal and vertical components. For this study, the horizontal component was ignored because the horizontal forces generated by opposing legs (e.g., left I vs. right IV) are approximately equal in magnitude and opposite in direction (hence the verticality of the jump).

Evasion model.—The premise underlying our evasion model was that an attack by a fish could be evaded by a fishing spider if the spider's jump occurred at the correct time relative to the attack and if the jump were high enough. In the geometric model (Fig. 1): (a) a fish attacked in a straight line at an angle (α) to the water surface and at a constant velocity (V_a); (b) throughout the attack, the trajectory of the fish was "aimed" at the location of the spider at rest on the water surface; that is, the center of the fish's open mouth followed a line that would have, had the spider remained stationary, intersected the center of mass of the spider when the spider was at rest; (c) the spider detected the approach of the fish at a distance (d_{det} , 0–2 cm), using sensors on the part of the spider (body or appendages) nearest to the fish, and began its vertical jump with a latency dictated by data collected in this study; (d) the spider jumped to a height (and with a duration) dictated by data collected in this study; (e) the attacking fish, a trout with attack velocities comparable to published fast start velocities of trout (*Oncorhynchus mykiss*: Domenici & Blake 1997) and with attack angles varying between 20–80°, attacked

with its mouth open and circular (radius: r , 1–2 cm); and (f) a successful evasion was defined as one in which the spider's center of gravity was outside of the fish's mouth ($d_{\text{ev}} > 0$) at the moment when the center of the mouth crossed the line representing the vertical trajectory of the spider. The attack angle (e, above) was constrained at the lower end by the fact that the spider would be invisible to the fish at angles less than the critical angle of the air-water interface, 48° (Denny 1993); we chose 20° both because we didn't want to underestimate a fish's ability to detect surface distortions even when it could not see through the surface, and because the fish's angle relative to the spider increases as the fish comes close to the spider. At the upper end, the attack angle was constrained by the recognition that, as the angle approaches 90°, a spider jumping vertically could not escape even if its jumps were 3× the highest jumps actually measured.

The model addressed two questions: for what angles of attack (α) and attack velocities (V_a) is spider jumping effective, and how do these parameters compare with actual velocities of attack by fish in the range of angles tested?

RESULTS

Data from high speed videography.—Videography at 1000 images/sec revealed that a jumping *Dolomedes* uses all eight legs, accelerated simultaneously downward, to propel itself into the air above the water surface (Fig. 2). During the propulsive part of the jump, each leg moves so rapidly (angular velocity = 3.36 ± 1.02 degrees/ms; mean ± 1 S.D.) that an air-filled cavity persists behind it throughout the interaction of leg and water (Fig. 3). The peak height that a spider's body reaches during a jump is determined primarily by its velocity at the end of the propulsive part of the jump. That velocity, in turn, is a consequence of the acceleration produced when a force exerted downward by the spider (= upward by the water) moves the mass of the spider. Thus, while the spider is in the air, its center of gravity should follow a parabolic path, decelerated by gravity as the spider rises and accelerated by gravity as the spider falls toward the water. In our study, the spider's paths were nearly perfectly parabolic (Fig. 4), with a characteristic small depression of the

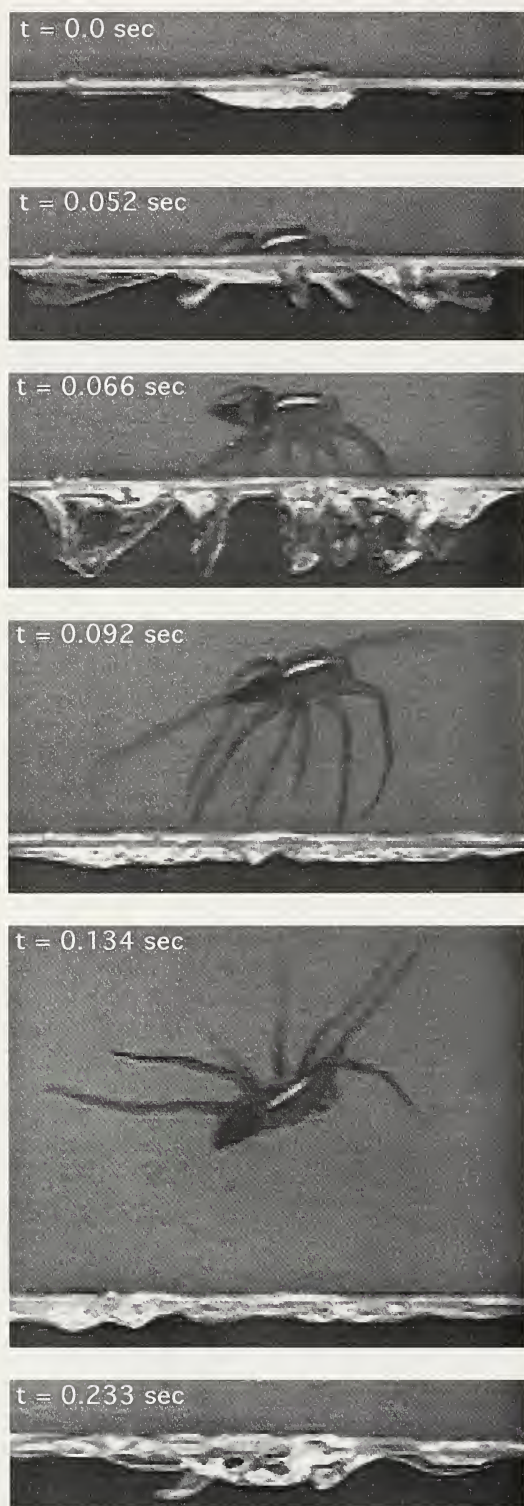


Figure 2.—High-speed lateral views of *Dolomedes* jumping vertically from the water surface. In an analysis of videographic images of a large (0.67 g) female, captured at 1000 frames/sec, the propul-

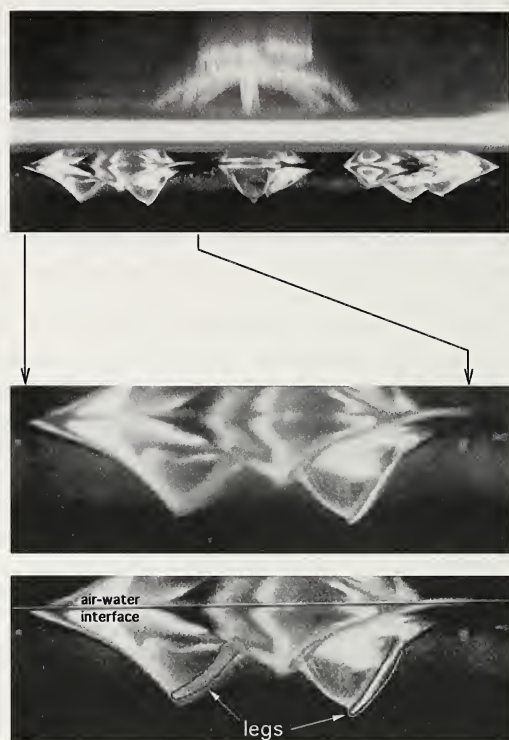


Figure 3.—Details of the sub-surface shapes of cavities formed during the propulsive phase of jumping by a smaller (0.32 g) female are revealed in an image captured on 35 mm film with electronic flash illumination (top). The tips of some tarsi protrude very slightly into the surrounding water. The location of two legs within air-filled cavities can be seen most clearly in the enhanced (bottom) image derived from the enlargement (center).

peak height because the center of gravity of each spider as a whole (legs included) varied with the positions of the legs, and the legs rose and fell relative to the body during a jump (Figs. 2, 4).

The digitization of body height as a function of time (Fig. 5, upper graphs) made it possible to calculate velocity ($\Delta\text{height}/\Delta\text{time}$) and plot velocity as a function of time (Fig. 5, lower graphs). During a jump, we used the downward motion of a leg tip (upper graph, dashed lines) to define the time during which

←

sive phase of the jump was completed within the first 90 ms, peak elevation was reached at about 134 ms, and the spider was out of contact with the water for about 141 ms.

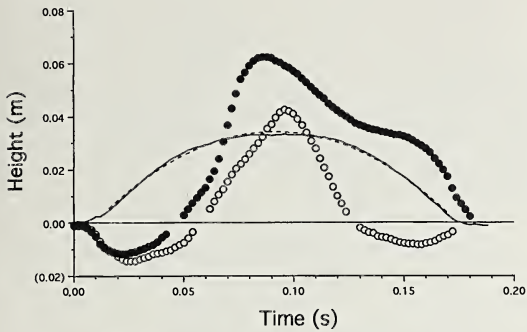


Figure 4.—Digitized tracks of a spider's approximate center of mass (solid line, “—”), the tarsus of a leg I (filled circles, “●”), and the tarsus of a leg IV (open circles, “○”), during a typical vertical jump from the water surface. The trajectory of the spider's center of mass follows nearly perfectly the parabola (dashed line, “—”) expected from gravitational mechanics. The sub-surface locations of the tarsi, during the initial 0.06 sec, indicate the propulsive phase of the jump.

propulsive acceleration occurred. For every two adjacent points in these graphs, we calculated the change in height as a function of elapsed time (vertical velocity). Plots of velocity versus time (lower graphs) showed roughly linear accelerations (slopes) for the propulsive and free-fall phases of the jumps: during propulsion, accelerations were rapid, approximately four times the acceleration of gravity; during freefall, calculated accelerations were within 5% of what was expected (9.8 m/s^2) for objects under the influence of gravity alone. In the jump of the larger spider, the steep negative acceleration that occurred between 0.015 and 0.045 sec is the result of the spider's legs rising from below to above its body (see Figs. 2 & 4), causing a rise in the spider's center of mass without a corresponding rise in the position of the spider's body.

Having measured multiple jumps of spiders of five different sizes, we were able to assess performance (i.e., jump height or time in free-fall) as a function of mass. A regression of time in freefall on mass (Fig. 6) revealed no

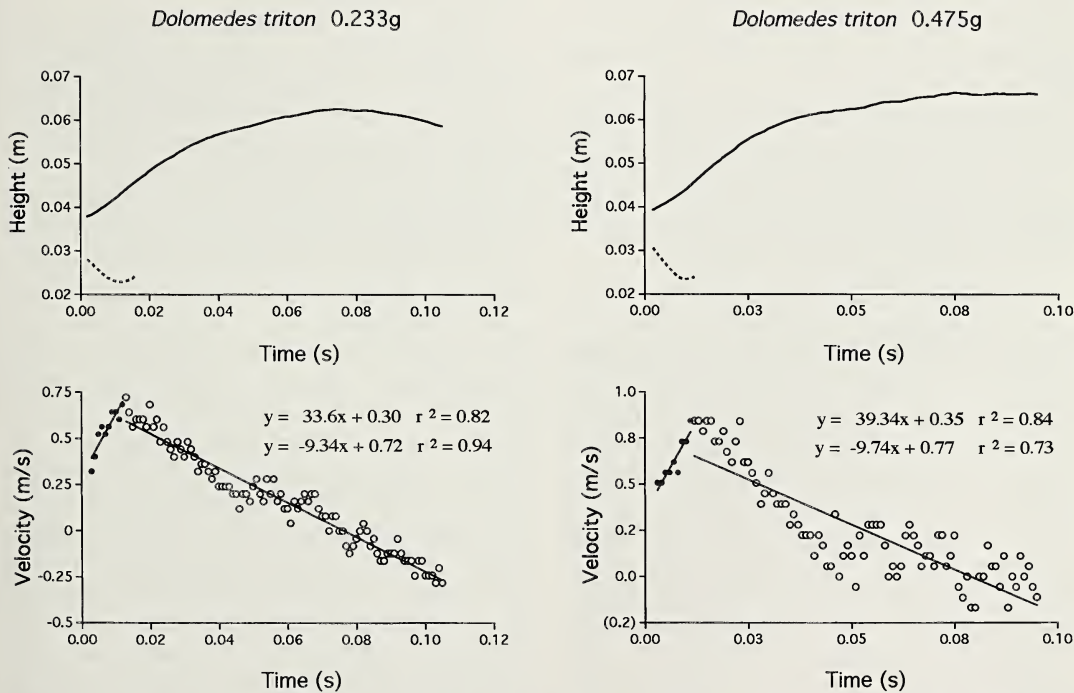


Figure 5.—Calculation of the accelerations due to the propulsive actions of the legs and due to gravity during free-fall. Changes in the height of the spider's center of gravity (upper graphs, solid lines) over time are caused initially by the downward push of the legs (upper graphs, dashed lines) and subsequently by the pull of gravity.

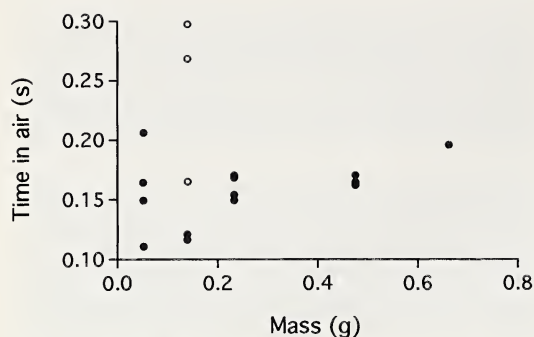


Figure 6.—The mass of a jumping spider does not influence the time the spider spends off of the water surface. The time spent aloft did not vary significantly with mass among females (filled circles, “●,” $r^2 = 0.21$, $n = 5$, $P > 0.05$; duration = 0.167 ± 0.046 sec, mean ± 1 S.D.) and could not be measured in our data from the single male (open circles, “○”).

significant relationship. Because time aloft and jump height are physically linked ($h = v_i t - gt^2/2$, where h is height, g is the acceleration of gravity, and t is time in the air), it follows that jump height is also relatively constant across sizes. This result is consistent with allometric measurements of jumping height in terrestrial mammals (Hill 1950; Pennycuik 1992).

Latency to jump (the time between the delivery of the stimulus and the first detectable downward movements of the spider's legs) did vary significantly with spider mass (Fig. 7): the largest spiders we tested were about 33% slower to respond than the smallest.

Because jump height and time in the air were approximately uniform across spider sizes (Fig. 6) and because larger spiders have more mass to accelerate, we assumed that the forces exerted by spiders during jumping would rise linearly with mass. This assumption was confirmed by our measurement of the force/leg used by spiders jumping vertically (Fig. 8, upper graph). The force used to accelerate a spider upward (“acceleration method”) rose significantly with mass (upper graph, solid line: for the pooled sexes, force = $4.52 \text{ mass} + 0.039$, $r^2 = 0.970$, $n = 5$, $P < 0.01$).

To investigate the contribution that surface tension may make to the water's resistance to the motion of the legs (and hence the spider's ability to push off from the water surface), we

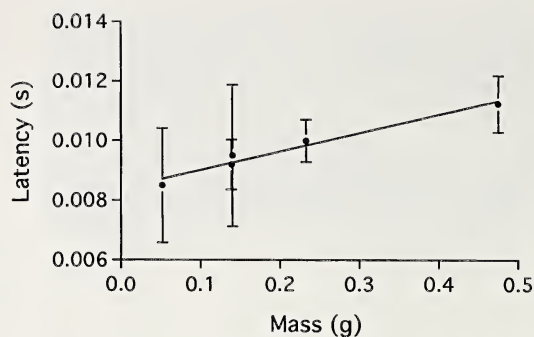


Figure 7.—Latency, the time between the stimulus and the first propulsive motions of the legs, rose significantly with mass (pooled sexes; latency = $0.006 \text{ mass} + 0.008$, $r^2 = 0.967$, $n = 5$, $P < 0.01$).

made calculations based upon the following premises: (a) the eight legs contribute equally to the support and vertical propulsion of the spider; (b) about half of each leg is in contact with the water during the propulsive phase of jumping (Fig. 2); (c) leg length is predictably related to spider mass (Suter & Wildman 1999); (d) maximum dimple depth is 3.8 mm (Suter & Wildman 1999).

Our calculations, using vertical forces derived from the “acceleration method,” revealed (Fig. 8, Table 1) that spiders of mass < 0.3 g could become airborne by simply pushing against the resistance caused by the dimples' combination of surface tension and buoyancy (curved, dashed line in Fig. 8, upper graph). Larger spiders, however, had to rely on drag resistance to generate the force necessary to propel them vertically. This difference in the importance of surface tension was also apparent in our force calculations, using vertical forces derived from the “leg-motion method,” concerning the jumps of a 0.05 g spider and a 0.75 g spider (Fig. 8, lower graphs). The vertical component of the force vector produced by the propulsive parts of the legs varied strongly with the angle of each leg relative to horizontal: as a leg approached 90° , the proportion of the force it could generate in a vertical plane approached zero. Not surprisingly, therefore, most of the useful force generation during a jump occurred when the legs were moving fast enough (e.g., not at the very beginning of a downward stroke) and were not at too steep an angle. For the larger of these spiders, the “submerged” portion of

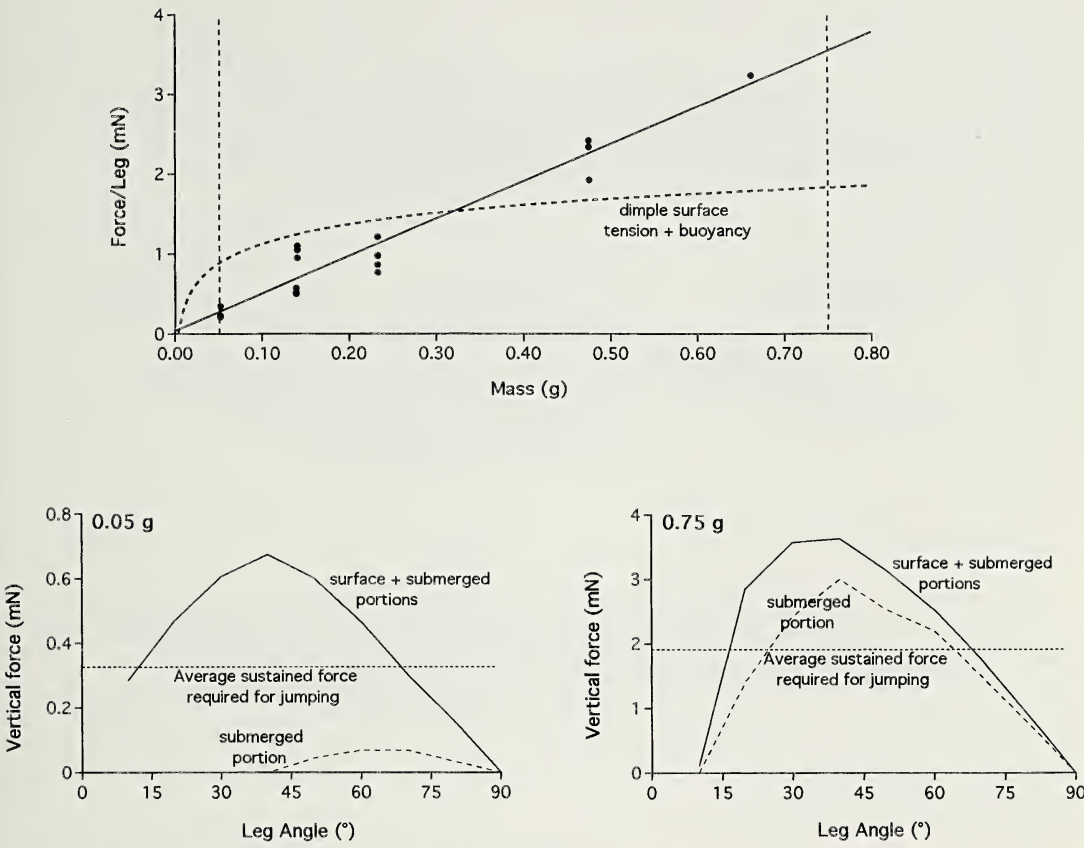


Figure 8.—Upper graph: The force used to accelerate a spider upward (“acceleration method”) rose significantly with mass (solid line, $r^2 = 0.970$, $n = 5$, $P < 0.01$), but only for spiders < 0.3 g was that force available from pushing against the resistance of the dimple (curved, dashed line). Lower graphs: The vertical component of the force vector produced by the propulsive parts of the legs (“leg motion method”) varies strongly with the angle of each leg relative to horizontal. Horizontal dashed lines represent the average force (“acceleration method”) required for a spider of the given mass to perform a jump of average height and duration. Vertical dashed lines in the upper graph mark the masses of the two spiders depicted in the lower graphs.

each leg (the part visible below the water surface in Fig. 3) made a major contribution to vertical force needed for a jump, whereas for the small spider, the submerged portion of the leg made a very small contribution.

Spider jumps in the context of fish strikes.—Our geometrical model (Fig. 1), designed to assess the efficacy of the vertical jump as a fish evasion behavior, combined our data on jump kinematics and latency with published data on trout fast start velocities (Domenici & Blake 1997). In the model, a successful evasion was one in which the spider’s center of mass was outside of the fish’s mouth as the strike trajectory of the fish crossed the jump trajectory of the spider.

When we plotted evasion distance (d_{ev} , cm) as a function of the angle of attack (α , degrees) and attack velocity (V_a , m/s), taking all $d_{ev} > 0$ as successful evasions, we found that even large variations in detection distance (0–2 cm) and spider size (0.06–1.0 g) did not render the spider safe at steep angles of attack or at strike velocities > 1 m/s (Fig. 9).

The maximum fast start velocities of trout (Domenici & Blake 1997), averaging 1.66 ± 0.48 (S.D.) m/s, are higher than the strike velocities at which spiders jumping vertically are safe (Fig. 10). Assuming that strikes have approximately the same peak velocities as fast starts, we conclude that only the most lethargic strikes by trout could be evaded by spiders.

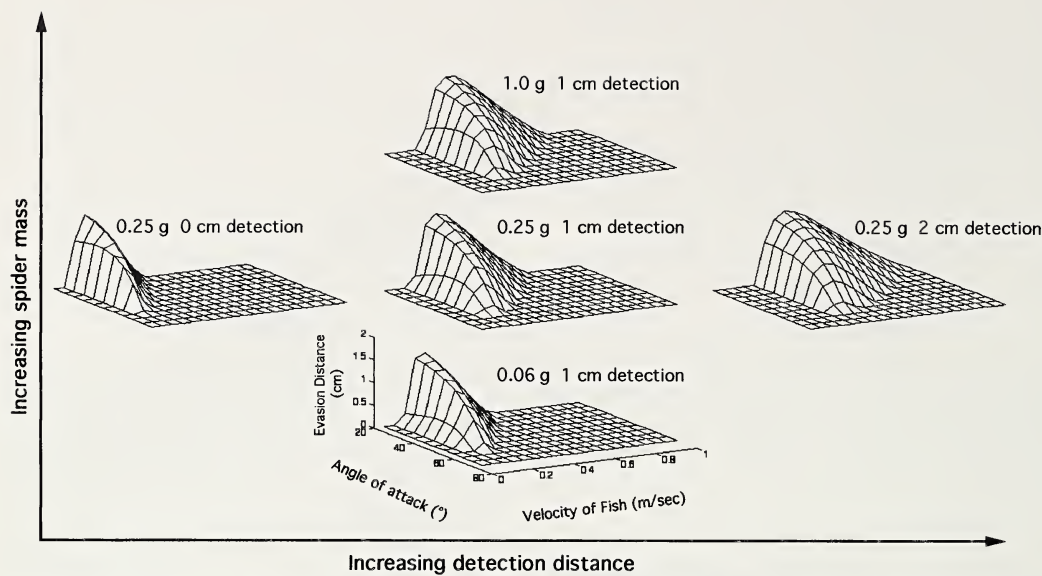


Figure 9.—Success of attack evasion. Evasion was deemed successful if the center of mass of the spider was outside of the trajectory of the trout’s mouth as the trout passed through the vertical trajectory of the spider. Thus, all positive values of evasion distance (vertical axis) constitute successful evasions. The evasion distance (d_{ev} , cm) was plotted as zero for negative values of d_{ev} (spider captured) to emphasize the difference between successful evasion and failure. In all situations, the velocity of the attacking fish and its angle of attack strongly influenced the efficacy of evasive jumping. Increases in the distance at which fish attacks could be detected, d_{de} , substantially increased the evasion success footprint, and increases in spider size had a similar effect.

Table 1.—Jumping from the water surface requires an upward force sufficient both to resist the downward pull of gravity and to accelerate the spider upward. Only for small spiders is the resistance offered by a dimple (surface tension plus buoyancy) sufficient for both (compare last two columns). Values in the last four columns are for a single leg and assume that all eight legs participate in vertical propulsion, that about half of each leg provides thrust, and that maximum dimple depth is 3.8 mm. Column 2, from equation 2, Suter & Wildman 1999; column 4, from regression in Fig. 8; column 6, from Suter & Wildman 1999.

Spider mass g	Estimated leg length mm	Force required for static support mN	Force required for jumping mN	Total resistive force required mN	Force available from dimple mN
0.050	11.5	0.061	0.265	0.326	0.875
0.150	17.8	0.184	0.717	0.900	1.271
0.250	20.8	0.306	1.169	1.475	1.437
0.350	22.7	0.429	1.620	2.049	1.555
0.450	24.1	0.551	2.072	2.623	1.662
0.550	25.3	0.674	2.524	3.198	1.733
0.650	26.3	0.796	2.976	3.772	1.792
0.750	27.1	0.919	3.428	4.346	1.816

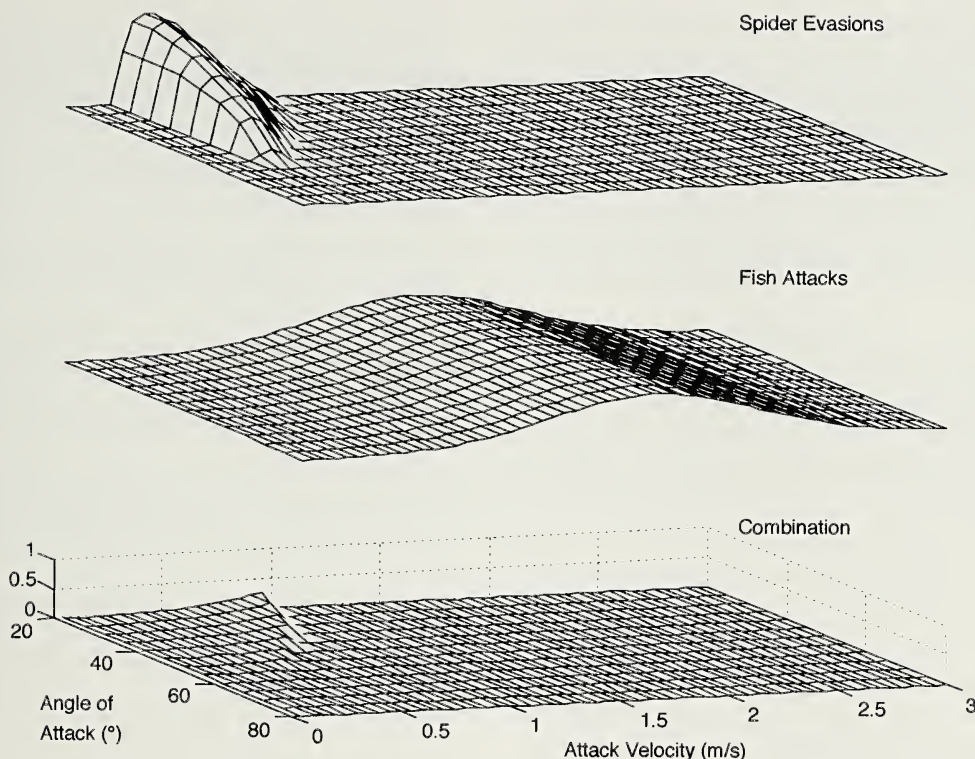


Figure 10.—Evasion success (top) and the actual attack dynamics of trout (middle), when combined, reveal a very small area of overlap on the velocity vs. angle-of-attack plane (bottom). This example depicts results for a 0.25 g spider with a 2 cm detection distance.

DISCUSSION

We began this study under the assumption that vertical jumps from the water surface by *D. triton* function to decrease the probability of capture by fish attacking from below. Implicit in our assumption was the presumed role that natural selection had played in shaping both jump latency and jump height (and duration), with the result that vertical jumping from the water surface, as currently practiced by fishing spiders, would be an effective evasive behavior. We have demonstrated, on the contrary, that jumping could save spiders in only a very small fraction of attacks by fish (Fig. 10). At the root of this ineffectual capacity are the size-independent maximum height of jumps (about 3.67 cm) and their correspondingly brief duration (about 0.17 sec), and at the root of the limited jump height is the quality of the interaction between the spiders' legs and the water.

Fluid drag ultimately provides the resistance against which the spider pushes (Fig. 8; Suter & Wildman 1999). It follows that ana-

tomical modifications to a spider's legs such as lateral expansions (via hairs or cuticular shape changes), which would expand the area of the surface perpendicular to the direction of the legs' motion during jumping, would increase drag and allow a more rapid upward acceleration of the spider. The more rapid acceleration would cause both jump height and jump duration to rise and would render the spider less vulnerable to predation by fish. The absence of such expansions suggests (a) that predation by fish constitutes a relatively mild selective force on these fishing spiders, (b) that contrary selective pressures (e.g., those fostering efficient rowing or prey capture) prevail, or (c) that lateral expansion is phylogenetically constrained. We have no data that allow us to discriminate among these three possibilities and note that any or all of them could operate simultaneously.

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PREDATORY INTERACTIONS BETWEEN MUD-DAUBER WASPS (HYMENOPTERA, SPHECIDAE) AND ARGIOPE (ARANEAE, ARANEIDAE) IN CAPTIVITY

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ABSTRACT. We report on efforts to maintain two common sphecid wasps, *Chalybion caeruleum* (Saussure 1867) and *Sceliphron caementarium* (Drury 1773), in field and laboratory enclosures in order to observe their predatory interactions with the orb-weaving spiders *Argiope aurantia* Lucas 1833 and *A. trifasciata* (Forskål 1775). Both species of wasps seemed to locate webs primarily by chance while flying along the tops of the vegetation but differed greatly in their hunting tactics once webs were located. *Sceliphron caementarium* was most successful at capturing spiders that had dropped out of webs in response to the wasp's hitting the web. But, *C. caeruleum* often employed a type of aggressive mimicry: it landed in the web or used its middle legs to pluck the web, luring the spider to the wasp. *Argiope* did not differ in their defensive response to *C. caeruleum* and *S. caementarium*. Most *Argiope* dropped out of webs in response to attacks rather than using other defensive behaviors such as shuttling between sides of webs or vibrating webs.

Keywords: Sympatry, competition, niche partitioning

Sphecid wasps are common predators of orb-weaving spiders. Because individual wasps capture several spiders to provision each cell in a nest and build multiple cells over their lives (Coville 1987), mud-dauber wasps can act as a particularly potent selective force on the evolution of spider defensive behaviors. Many studies have examined the numbers and species of spiders provisioned in wasp nests, providing insight into which spiders may be most vulnerable to wasps (e.g., Muma & Jeffers 1945 and references in Krombein et al. 1979). These studies indicate that different species of wasps that hunt in the same habitat, such as *Chalybion caeruleum* and *Sceliphron caementarium*, often catch different prey. This suggests that sympatric species of sphecids may employ different predatory tactics, perhaps due to niche partitioning. There are few, mostly anecdotal, observations on the hunting tactics of sphecids (Peckham & Peckham 1905; Rau 1928, 1935; Eberhard 1970; Endo 1976; Coville 1987; Rayor 1997). But, there has been no comparative study of the hunting behaviors of sympatric *C. caeruleum* and *S. caementarium*.

Little is known about the primary and secondary defensive behaviors orb-web spiders use against sphecids. Yet, it is the interaction of spider defensive behaviors and the predatory tactics of wasps that determine if individual spiders survive predation attempts (Cloudsley-Thompson 1995; Edmunds & Edmunds 1986; Tolbert 1975). There are two detailed studies of wasp-spider interactions, but these focus on wasps hunting nocturnal or colonial orb-weaving spiders (Eberhard 1970; Rayor 1997). What is missing, therefore, are studies of the interactions of wasps with solitary, diurnal spiders, such as *Argiope*.

Argiope is among the most intensively studied genera of spiders and is likely to be particularly vulnerable to visually-hunting predators because it rests at the center of its web during daylight. *Argiope* is also an important model for testing hypotheses concerning possible defensive functions of structures such as barrier webs (Higgins 1992) or stabilimenta (Blackledge & Wenzel 1999). Here we report on our efforts to maintain two species of sphecid wasps (*C. caeruleum* and *S. caementarium*) in field and laboratory enclosures and our observations of their predatory interactions with the orb-weaving spiders *Argiope aurantia* and *A. trifasciata*.

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METHODS

We observed the hunting behaviors of *C. caeruleum* and *S. caementarium* in one indoor enclosure (1998 and 1999) and three outdoor enclosures (1999). All wasps were collected as adults in the field (Dublin, Ohio), except for a single *C. caeruleum* that emerged from a previously collected nest during the 1998 study. The collection site consisted of old barns surrounded by old fields. The primary prey caught by wasps at this site were immature *A. trifasciata* (pers. obs.). Individual wasps were distinguished by paint on the thorax or abdomen.

The $3.4 \times 2.7 \times 2.2$ m screened indoor enclosure was located in Ohio State University's Insectary, Columbus, Ohio, in a greenhouse room with light and temperature maintained near outdoor levels. Assorted plants, including flowering *Echinacea* (Asteraceae) and *Lantana* (Verbenaceae), were scattered throughout the enclosure to provide resting places for wasps. The plants also simulated the natural background of foliage in which wasps hunt spiders, a potentially important feature of the study because background may influence the conspicuousness of spider silks to insects (Blackledge 1998a; Blackledge & Wenzel 2000). A 20×30 cm plastic pan was placed in one corner of the enclosure and contained a layer of earth from the same pond at the field site where wild *S. caementarium* collected mud for their nests. The pan was partially filled with water and then tilted to create a moisture gradient from completely saturated to nearly dry, simulating the bank of the pond. Mud nests of *S. caementarium*, collected at the field site, were glued to wooden boards in the upper corners of the enclosure to encourage building of new nest cells by *S. caementarium*. These nests also provided vacant cells for *C. caeruleum*, which nests only in abandoned *S. caementarium* cells (Rau 1928). In 1998, petri dishes containing a sucrose and honey mixture were placed on the floor of the cage to provide wasps with a nectar source. In 1999, a plastic hummingbird feeder filled with a 1:1 honey:water solution was used instead. The honey water was changed every two days to prevent fermentation.

The three outdoor enclosures consisted of nylon screening over wood frames ($3.8 \times 2.3 \times 2.0$ m) and were located in a field at Ohio

State University's Rothenbuhler Honeybee Laboratory, Columbus, Ohio. We found it necessary to cover the bottom edge of the screening with thick layers of bark mulch and stone to prevent wasps from crawling under the edges of the enclosures. The natural ground cover consisted of various grasses (Poaceae) and thistle (Asteraceae), with a thick layer of thatch. There were some naturally occurring *A. trifasciata* in the surrounding field. Again, each enclosure had a 20×30 cm plastic pan containing mud and water, wooden boards with mud *S. caementarium* nests glued to them, and a hummingbird feeder as a nectar source.

Immature *A. aurantia* and *A. trifasciata* were collected from roadside ditches in and around Columbus. Most of the spiders were uniquely marked and weighed immediately after collection. Spiders were allowed to build their webs in $35 \times 35 \times 10$ cm wooden frames as described in Blackledge (1998b) but modified with both plastic sides being removable. We placed individual frames containing spiders within the enclosures to observe wasp-spider interactions. We recorded our observations on audio tape and also video-taped a few of the encounters. We also include some observations on *A. trifasciata*, in webs on natural plant supports, which we placed in the same outdoor enclosures and one of us (TAB) used for a second study examining the role of stabilimenta as wasp defenses. We released a variety of araneid, linyphiid and tetragnathid spiders into the indoor enclosure to provide alternative prey, while the outdoor enclosures naturally contained a variety of agelenids, salticids and thomisids as well as *Cyclosa conica* (Pallas 1772) and *Uloborus glomosus* (Walckenaer 1841). Because we later found few individuals of these species in wasp nests (10 of 142 excavated spiders) and we never directly observed a predation event involving these species, we exclude them from further discussion.

RESULTS

In the indoor enclosure, we observed 24 attempted predation events during 20 days of observation (between 4–28 August 1998 and between 28 July–17 August 1999). In the outdoor enclosures, we observed 50 predation attempts during observations every day between 21 August and 11 September 1999. *Chalybion*

Table 1.—Predatory tactics of two species of sphecid wasp, *C. caeruleum* and *S. caementarium*, and the common defensive responses by immature *A. aurantia* and *A. trifasciata*. Observations were made on 3 individuals of *C. caeruleum* and 5 individuals of *S. caementarium*. The heading “Spider approached wasp” includes approaches by spiders to either wasps landing in webs or plucking webs. Defensive responses of spiders were not mutually exclusive. Asterisks denote significant differences, using binomial probability, between species of wasps in frequency of behaviors (*P < 0.05, **P < 0.01, ***P < 0.005).

	<i>C. caeruleum</i>	<i>S. caementarium</i>
Observed attacks	48	26
Location of capture:		
web center	6	3
capture zone or frame threads	14	6*
ground below web	4	11**
Total	24	20
Wasp landed in web	22	3***
Wasp plucked web	11	0**
Spider approached wasp	15	1**
Response of spider:		
drop from web	21	15
abandon web	7	7
move to web periphery	15	6
Mass of spiders captured:		
mean ± standard deviation	0.04±0.01 mg	0.04±0.02 mg
range	0.02–0.07 mg	0.02–0.08 mg

caeruleum opened their nests and began hunting between 1000–1200 h and resealed their nests between 1400–1700 h or, if no spiders were captured, after only 30 min. *Sceliphron caementarium* typically opened nests for the entire day (1000–1700 h). Like other sphecids, both *C. caeruleum* and *S. caementarium* often did not hunt on overcast, rainy days and became active much later than normal on cooler days (see also Freeman & Johnston 1978; Powell 1967). Encounters were sometimes brief—lasting only a few seconds if spiders were caught at the centers of webs, and sometimes much longer, lasting 2–3 min if spiders attempted to escape by dropping and then moving rapidly through the grass. We combined all of the data for each species of wasp (Table 1) and, within each species, we had approximately the same number of observations for each individual wasp. We only included observations on predation attempts on spiders that were within the size range captured by wasps during the experiment (Table 1).

Both wasp species seemed to locate webs by chance while flying along the top of the vegetation in a seemingly haphazard flight

path. However, *S. caementarium* and *C. caeruleum* differed greatly in their hunting tactics once webs were located (Table 1). *Sceliphron caementarium* bumped into webs while flying, but then flew off without seeming to react to webs as anything other than physical barriers. But, these wasps vigorously pursued spiders that dropped from webs, spending as much as 2–3 min crawling around the thatch and grass stems under webs in gradually enlarging circular patterns until either spiders were located or wasps began flying again.

In contrast *C. caeruleum* often landed in webs or on the substrate supporting webs and then used their middle legs to pluck the silk. When in a web, *C. caeruleum* sometimes contracted its entire body every few seconds for up to two minutes. In 68% of these instances, spiders ran to wasps after wasps had landed in or plucked at webs. Many of these spiders (70%) were caught as they approached wasps or as wasps chased them back to the centers of webs, but others immediately dropped out of webs upon contacting wasps.

Captured spiders were stung between the carapace and sternum in the posterior of the cephalothorax. Paralysis appeared to be in-

stantaneous, but spiders were occasionally stung multiple times, stings lasting up to a few seconds. Wasps carried spiders by holding the pedipalps in their mandibles, with the venters of spiders facing toward the venters of wasps. Wasps commonly pressed their mandibles against the chelicerae of spiders for a few seconds after capture, perhaps drinking hemolymph. After about 25% of captures, both species of wasp drank hemolymph from the chelicerae or coxae of spiders for periods of up to 1 min. Four of those spiders were subsequently discarded instead of being used to provision a nest.

We observed 9 instances (not in Table 1) where a wasp attacked a spider, grasped the spider with its legs, wrapped its abdomen around the spider as though stinging it, but then released the spider and flew away. In each instance the spider was still alive and ran away when touched by one of us. All but two of those spiders weighed within the mean ± 2 standard deviations of *Argiope* captured during the study.

DISCUSSION

Eberhard (1970) concluded that contrast between a spider and the background upon which it rested was one of the most important cues used by *S. caementarium* to locate *Larinioides* (*Araneus*) *cornutus* (Clerk 1757), which were hiding in retreats near webs. In our study, both *C. caeruleum* and *S. caementarium* often alighted upon dark spots of debris or the shadows of insects or spiders on the opposite side of the screen tent, which supports Eberhard's hypothesis that wasps respond to contrast. However, *S. caementarium* attacked very few spiders at the centers of webs, instead seeming to stumble into and out of webs without regard for the possible presence of spiders. *Chalybion caeruleum* and *S. caementarium* often flew within 2 cm of spiders on webs or grass, without reacting to the spiders, but quickly chased spiders once spiders dropped from or moved within webs. Both of these observations suggest that contrast was not actually used to locate *Argiope* in our study. There are at least two potential explanations for this difference with Eberhard's findings. The light-colored bodies of juvenile *Argiope* may reflect significant UV light (Craig & Ebert 1994), and this may provide a poor contrast against natural back-

grounds to insects, much as stabilimentum silk can (Blackledge 1998a; Blackledge & Wenzel 2000). Another possible explanation is that motion may be an important cue in eliciting attacks by *S. caementarium*. This second explanation seems particularly likely because *S. caementarium* pounced on small moving insects or even falling debris, particularly when wasps were searching for spiders flushed from webs.

Sceliphron caementarium aggressively pursued spiders that dropped from webs, catching most prey by chasing spiders on the ground, while *C. caeruleum* used aggressive mimicry to catch spiders that were still in webs (Table 1). *Chalybion caeruleum* landed in webs and then plucked at the silk in webs, luring spiders to themselves. In almost 70% of encounters where *C. caeruleum* landed in or plucked webs, spiders approached wasps; and most of those spiders were captured with little chase. We even observed one instance where a spider, which had dropped out of its web into the grass, proceeded to crawl back up its dragline to the web center and then to a *C. caeruleum* as the wasp plucked the web. This plucking behavior is similar to that described for *Chalybion* spp. (Schwarz, in Howard 1901; Coville 1976) and *Trypoxylon* sp. (Rau 1926; pers. obs.) and may be a particularly effective method to hunt retreat dwelling spiders (Coville 1976). One vespid is also thought to use vibrations caused by tapping with its antennae to lure spiders to the hubs of webs (MacNulty 1961).

Sceliphron caementarium nests contain a wider range of spider prey than the nests of *C. caeruleum*. *Sceliphron caementarium* provisions nests with both web-building and curatorial spiders, while the nest contents of *C. caeruleum* are largely restricted to orb and tangle web-building spiders (Krombein et al. 1979; Muma & Jeffers 1945). These differences in nest provisioning likely reflect the different hunting tactics used by these two species of wasps. The use of old *Sceliphron* nests by *Chalybion* (Rau 1928) restricts *Chalybion* to hunting in habitats occupied by *Sceliphron*. Thus, competition has likely been an important selective factor in the evolution of *Chalybion* and *Sceliphron* hunting behaviors. Therefore, the specialization on web-building spiders by *Chalybion* could be due to niche partitioning.

Argiope used similar defensive behaviors against both species of wasps (Table 1). The most common response to attacks was for spiders to drop from webs (50% of encounters) and then either freeze or run to nearby cover. Spiders often maintained contact with their webs via draglines and returned 2–10 min later. But, spiders sometimes abandoned webs completely, moving up to 1 m away, in deep grass. *Argiope trifasciata* on natural webs built in the grassy outdoor enclosures also sometimes abandoned webs when attacked. They would then build webs in new locations the next day, without having consumed the abandoned web. These observations suggest that field researchers should use caution when assuming that abandoned webs always indicate predation, because abandoning webs is itself a defensive strategy.

Occasionally a spider ran to the top or side of its web (30% of encounters), remaining motionless for up to several minutes before returning to the web center. Spiders that remained at web hubs often stilted, holding their bodies far out from webs and angling their abdomens away from the plane of webs. We suggest that these defensive behaviors might be relatively specialized responses to wasp predators (see also Cushing & Opell 1990), because spiders did not engage in other common defensive behaviors such as web flexing or shuttling (Cloudsley-Thompson 1995; Edmunds & Edmunds 1986; Tolbert 1975). Web flexing is often initiated when humans approach webs (pers. obs.) and may function against salticid predators (Tolbert 1975) but was never used against wasps. While our observations supplement descriptive works on the behavioral interactions of wasps and spiders, we hope that the use of enclosures will also facilitate a more experimentally-based approach to the study of wasp-spider interactions.

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SPIDERS IN ROCKY HABITATS IN CENTRAL BOHEMIA

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ABSTRACT. Spiders of andezite and limestone rocks in Central Bohemia were studied. The material was collected using hanging desk traps. Rocky habitats are inhabited by a well-established spider assemblage. A lower slope angle, and consequently more diverse terrain, probably support a higher species diversity. Some species inhabit exclusively rocky habitats. *Segestria bavarica* and *Theridion betteni* occur in the Czech Republic exclusively on rocky habitats. *Erigonoplus jarmilae*, *Zelotes puritanus*, and *Altella biuncata* appear to occur primarily on rocky habitats. *Anyphaena furva* appears to live on trunks of trees growing on sun-exposed rocks. Some thermophilous species narrow their ecological niche exclusively to southern exposed rocky habitats with a warm microclimate towards the north.

Keywords: Spiders, rocks, vegetation-free habitats, thermophilous species

The lowlands of Central Europe were originally covered mostly with closed forests, although isolated islet-like natural non-forest habitats occasionally occurred. Today the surface of some of these non-forested areas is composed of bare bedrock or products of its erosional breakdown (without a soil layer) and are typified by gravel and sand banks, sand dunes, scree slopes and rock outcrops. According to their specific substratum and microclimate, these habitats can harbor specialized spider species.

There has been no comprehensive study of the spiders of gravel banks in the Czech Republic. However, useful data were obtained during the grid mapping of lycosid distribution by Buchar (1995); and gravel and sand banks are known to harbor several specific inhabitants. Of these, *Oedothorax agrestis* (Blackwall 1853) is the most common, *Pardosa morosa* (L. Koch 1870) occurs sporadically, while *Arctosa cinerea* (Fabricius 1777) and *Arctosa maculata* (Hahn 1822) are very rare.

There is also a need for a detailed study of the spiders of sand dunes in the Czech Republic. However, the specific arachnofauna of this habitat is known. *Arctosa perita* (Latreille 1799), *Steatoda albomaculata* (De Geer 1778), and *Attulus saltator* (Simon 1868) represent specialized inhabitants of sand dunes (Miller 1971; Buchar 1995). New investigations of sand dunes in southern Moravia have resulted in several new records for the Czech

Republic (Růžička 1998): *Uloborus walckenaerius* Latreille 1806, *Mecynargus foveatus* (Dahl 1912) and *Titanoeca psammophila* Wunderlich 1993.

Scree slopes have been intensively studied over the past years, and microclimate conditions and spider assemblages have been described (Růžička & Zacharda 1994; Růžička et al. 1995). *Acantholycosa norvegica sudetica* (L. Koch 1875), *Bathypantes simillimus buchari* Růžička 1988, *Lepthyphantes improbulus* Simon 1929 and *Wubanoidea uralensis* (Pakhorukov 1981) are the most specific inhabitants of boulder accumulations in the Czech Republic (Růžička 1996; Růžička & Hajer 1996; Růžička & Zacharda 1994).

Rock faces, rock walls, solitary rock outcrops and rocky slopes in deeply-cut river valleys remain some of the most inaccessible and unknown habitats. Due to the difficulty of exploiting them economically, these habitats have remained unchanged over the entire Holocene. The plant and animal communities inhabiting them represent edaphic climaxes. The aim of this study was to describe and evaluate the species composition of a spider assemblage in two different rocky habitats in the warmest territory in Central Bohemia.

METHODS

Study sites.—Both localities studied lie in Central Bohemia, on the border of Thermophyticum and Mesophyticum, and both are at similar elevations with similar exposures. Nezabudické Skály (rocks) Nature Reserve is

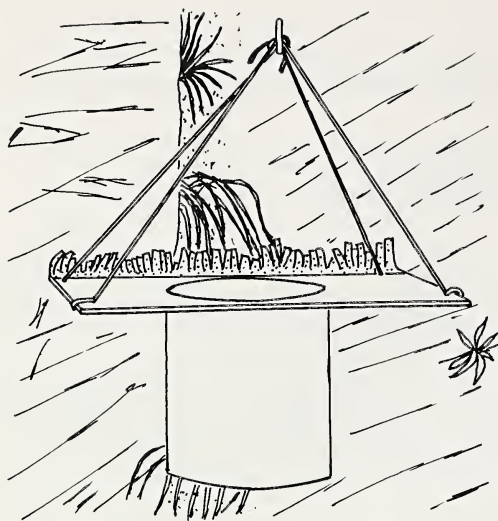


Figure 1.—Traps, as shown above, hanging against the creviced and rough rock surfaces, were used to capture the spiders. They contained a mixture of formaldehyde and glycerol.

situated in the Křivoklátsko Biosphere Reserve, near Nezabudice village, about 50 km west of Prague, elevation 290 m. The rocks are composed of andezite and form a southeasterly exposed amphitheater. The western part of this amphitheater is formed by bare rocks, small scree fields and narrow scree ledges with plant tussocks, shrubs and solitary trees. The rocky slope is about 60 m high with a slope angle of about 45°.

Kotýz National Nature Monument is situated in the Bohemian Karst Protected Landscape Area, near Koněprusy village, about 30 km southeast of Prague, elevation 380 m. The vertical southern exposed rock wall is made of limestone. It is about 40 m high and is partly overgrown by plant tussocks.

We automated the collecting of spiders on rocks using hanging desk traps (Růžička & Antuš 1997) (Fig. 1). The traps, made of rigid plastic, consist of a desk (25 × 20 cm, which formed an artificial horizontal surface) and a can (13 cm high and 10.5 cm in diameter) inserted in the center of the desk. The traps contained a mixture of 7% formaldehyde and 10% glycerol with a few drops of a surfactant. Each trap was hung from a hooked nail. A band of emery tape was stuck on the back edge of the trap and shaped to form a connection, or transit, between the desk and the rock surface. We hung the traps in marginal,

creviced, and rough parts of the rocks in the mosaic of bare rock surface and vegetation tussocks. Six traps were placed in Nezabudické Skály from May 1996 to April 1997, and in Kotýz from May to October 1996. Five additional desk traps with a half-circle back margin were hung on old oaks growing at Nezabudické Skály from April to June 1997.

The material was evaluated with respect to the occurrence of the species in phytogeographical regions and in habitats of various degree of originality (Buchar 1993) (see legend of Table 1). The nomenclature follows the check list of spiders of the Czech Republic (Buchar et al. 1995).

RESULTS AND DISCUSSION

Species diversity.—A total of 218 determinable spider individuals belonging to 48 species was collected on rocks at Nezabudické Skály. A total of 102 determinable spider individuals belonging to 27 species was collected at Kotýz. A total of 30 spider individuals belonging to 10 species was collected on tree trunks at Nezabudické Skály (Table 1).

Fourteen common species and a common dominant species, *Drassodes lapidosus*, reflect the similarity of both sites. The localities studied differ in the type of rock and in the slope angle. The higher number of species and individuals at Nezabudické Skály is probably caused by a greater diversity of terrain conditions resulting in more niche diversity. Lower slope angle allows the occurrence of small scree fields, small ledges, and consequently rich plant tussocks, solitary shrubs and trees.

The frequency of specimens of species occurring primarily in natural habitats amounts to 0.41 at Nezabudické Skály, and 0.45 at Kotýz, which is considerably higher than the minimal value of 0.20 that is characteristic for protected regions in the Czech Republic (Růžička 1987). High frequency of these species indicates original habitats.

Rock as a habitat.—Hänggi et al. (1995) distinguish 85 habitat types in their classification of Central European habitats. They include only the habitat "Alpine rocks" in the category of "Alpine habitats." The rocks of lower elevations are omitted. However, there are spider species that live occasionally, primarily, or exclusively on rocks. Heimer & Nentwig (1991) and also Miller (1971) described rocks as living habitat for about 20

Table 1.—Survey of material collected ($\delta/\varphi/j$) by hanging desk traps on rocks at Nezabudické Skály (A), on tree trunks at Nezabudické Skály (B), and on rocks at Kotýz (C). T = occurring primarily in Thermophyticum, M = in Mesophyticum, O = in Oreophyticum, N = non-specific; 1 = occurring in natural habitats corresponding to climatic or edaphic climax, 2 = capable of occupying some shadow and wet secondary, semi-natural habitats (cultural forests, shrubs, cultivated wetlands), 3 = capable of forming viable populations in artificially deforested, man-made habitats (fields, meadows, urban habitats).

			A	B	C
Segestriidae					
T	1	<i>Segestria bavarica</i> C. L. Koch 1843	3/—	—	—/1/1
Dysderidae					
N	2	<i>Harpactea hombergi</i> (Scopoli 1763)	1/—	1/9	1/—
Eresidae					
T	1	<i>Eresus cinnaberinus</i> (Olivier 1789)	—	—	2/—
Theridiidae					
T	1	<i>Dipoena melanogaster</i> (C. L. Koch 1837)	—	—	1/1
?	1	<i>Dipoena nigroreticulata</i> (Simon 1879)	—/1	—	—
N	2	<i>Episinus truncatus</i> Latreille 1809	—	—	—/1
T	1	<i>Theridion betteni</i> Wiehle 1960	—/1	—	—
N	2	<i>Theridion tinctum</i> (Walckenaer 1802)	—	1/—	—
Linyphiidae					
N	3	<i>Araeoncus humilis</i> (Blackwall 1841)	—/1	—	—
N	2	<i>Bathypantes nigrinus</i> (Westring 1851)	—/1	—	—
O	2	<i>Centromerus sellarius</i> (Simon 1884)	1/1	—	—
N	3	<i>Centromerus sylvaticus</i> (Blackwall 1841)	1/—	—	—
N	3	<i>Dicymbium nigrum</i> (Blackwall 1834)	2/1	—	—
T	1	<i>Erigonoplus jarmilae</i> (Miller 1943)	15/5	—	—
N	2	<i>Lepthyphantes flavipes</i> (Blackwall 1854)	2/—	—/1	—
T	1	<i>Lepthyphantes keyserlingi</i> (Ausserer 1867)	2/—	—	2/—
N	3	<i>Lepthyphantes mengei</i> Kulczyński 1887	1/—	—	—
N	2	<i>Lepthyphantes pallidus</i> (O. P.-Cambridge 1871)	—/1	—	—
N	3	<i>Linyphia triangularis</i> (Clerck 1757)	—/1	—	—
N	3	<i>Micrargus subaequalis</i> (Westring 1851)	—	—	1/—
N	2	<i>Microneta viaria</i> (Blackwall 1841)	2/—	—	—
N	1	<i>Panamomops affinis</i> Miller & Kratochvíl 1939	1/—	—	—
Tetragnathidae					
N	3	<i>Pachygnatha degeeri</i> Sundevall 1830	—	—	1/—
Araneidae					
T	1	<i>Gibbaranea bituberculata</i> (Walckenaer 1802)	—	1/—	—
N	3	<i>Mangora acalypha</i> (Walckenaer 1802)	—/—/2	—	—/1
Lycosidae					
T	2	<i>Alopecosa accentuata</i> (Latreille 1817)	5/1	—	—
T	1	<i>Arctosa figurata</i> (Simon 1876)	—	—	1/—
?	1	<i>Pardosa alacris</i> (C. L. Koch 1833)	2/2	—	5/3
T	1	<i>Pardosa bifasciata</i> (C. L. Koch 1834)	—	—	3/3
T	1	<i>Trochosa robusta</i> (Simon 1876)	1/1	—	—
M	3	<i>Trochosa ruricola</i> (De Geer 1778)	6/1	—	—
N	2	<i>Xerolycosa nemoralis</i> (Westring, 1861)	6/—	—	4/—
Agelenidae					
O	2	<i>Histoipona torpida</i> (C. L. Koch 1834)	2/—	—	—
N	2	<i>Textrix denticulata</i> (Olivier 1789)	6/—/1	—	—

Table 1.—Continued.

			A	B	C
Dictynidae					
T	1	<i>Altella biuncata</i> (Miller 1949)	5/—	—	—
Amaurobiidae					
O	2	<i>Callobius claustrarius</i> (Hahn 1833)	1/—	—	—
O	2	<i>Coelotes inermis</i> (L. Koch 1855)	4/—	—	—
N	2	<i>Coelotes terrestris</i> (Wider, 1834)	1/—	—	—
Titanoeceidae					
T	1	<i>Titanoeca quadriguttata</i> (Hahn 1833)	1/—	—	7/2
Anyphaenidae					
M	1	<i>Anyphaena furva</i> Miller 1967	—	3/—	—
Liocranidae					
N	2	<i>Apostenus fuscus</i> Westring 1851	1/—	—	—
N	3	<i>Liocranum rupicola</i> (Walckenaer 1830)	—	1/—	—/—/2
N	2	<i>Phrurolithus festivus</i> (C. L. Koch 1835)	—	—	1/—
Clubionidae					
N	1	<i>Clubiona comta</i> C. L. Koch 1839	—	1/2	—
Zodariidae					
T	1	<i>Zodarion germanicum</i> (C. L. Koch 1837)	1/1	—	—
Gnaphosidae					
T	1	<i>Callilepis schuszeri</i> (Herman 1879)	2/3	—	—
N	2	<i>Drassodes lapidosus</i> (Walckenaer 1802)	34/4	6/2	37/4
T	1	<i>Drassyllus villicus</i> (Thorell 1875)	1/1	—	—
N	1	<i>Echemus angustifrons</i> (Westring 1862)	1/—	—	—
T	1	<i>Gnaphosa opaca</i> Herman 1879	5/1	—	—
T	1	<i>Zelotes erebeus</i> (Thorell 1870)	2/1	1/—	—
?	1	<i>Zelotes exiguus</i> (Müller & Schenkel 1895)	5/3	—	—
T	1	<i>Zelotes puritanus</i> Chamberlin, 1922	7/4	—	—
Thomisidae					
M	1	<i>Ozyptila blackwalli</i> Simon, 1875	—	—	1/—
T	1	<i>Ozyptila nigrita</i> (Thorell 1875)	2/—	—	—
M	3	<i>Xysticus kochi</i> Thorell 1872	6/3	—	1/—
T	1	<i>Xysticus ninnii</i> Thorell 1872	—	—	3/—
Salticidae					
T	2	<i>Aelurillus v-insignitus</i> (Clerck 1757)	14/3/2	1/—	—
?	1	<i>Heliophanus aeneus</i> (Hahn 1831)	6/—	—	—
T	2	<i>Heliophanus cupreus</i> (Walckenaer 1802)	1/—	—	1/—
T	1	<i>Pellenes tripunctatus</i> (Walckenaer 1802)	—	—	1/—
T	1	<i>Philaeus chrysops</i> (Poda 1761)	3/—	—	6/—
T	1	<i>Phlegra festiva</i> (C. L. Koch 1834)	—	—	1/—
N	3	<i>Salticus scenicus</i> (Clerck 1757)	2/2/1	—	1/—
T	1	<i>Sitticus penicillatus</i> (Simon 1875)	—	—	—/1
M	3	<i>Sitticus pubescens</i> (Fabricius 1775)	2/2	—	1/—

spider species. Růžicka (1992) described the spider assemblage inhabiting sandstone rocks in northern and northeastern Bohemia. *Bathypantes similimus* inhabits, exclusively, these sandstone rocks in Central Europe, *Lep-*

thyphantes pulcher inhabits not only sandstone, but also granite and limestone rocks. *Drassodes lapidosus* was the dominant species in both localities studied; this species is generally considered to live under stones. The

occurrence of *Segestria bavarica*, *Theridion betteni*, *Tetrax denticulata*, and *Salticus scenicus* on rocks is mentioned by Miller (1971). The first two species occur exclusively on rocks in the Czech Republic. Abundant occurrence of *Titanoeca quadriguttata*, *Callilepis schuszteri*, *Gnaphosa opaca*, *Zelotes exiguus*, and *Aelurillus v-insignitus* at localities studied indicates that these species are well able to colonize rocky habitats. The abundance of *Erigonoplus jarmilae*, *Zelotes puritanus*, and *Altella biuncata* at Nezabudické Skály indicates that they occur primarily on rocky habitats. During intensive research of xerotherm localities in the Czech Republic, six specimens of *Zelotes puritanus* were collected at forest steppes (Miller & Buchar 1977; Šinková 1973). Šmaha (1983) collected 12 specimens at steppe slopes with isolated rocks in Křivoklátsko Biosphere Reserve, while we obtained 11 specimens; 14 specimens of *Erigonoplus jarmilae* were collected at rock steppes (Miller 1947; Valešová 1962), we obtained 20 specimens; 5 specimens of *Altella biuncata* were collected on rock steppes and rocky slopes (Miller 1949; Buchar 1989; Dolanský 1997), we obtained 5 specimens.

The occurrence of *Zelotes puritanus* (= *Zelotes kodaensis* Miller & Buchar 1977) in Europe is known in the Czech Republic, Poland (Staręga 1972) and Austria (Thaler 1981). This species inhabits exclusively original habitats, rocks and rock steppes here. This species cannot represent a recent introduction into Europe (Platnick & Shadab 1983). In North America *Zelotes puritanus* inhabits a wider range of habitats. Specimens have been collected in pitfall traps in aspen, fir, scrub oak, lodgepole, ponderosa pine, black spruce forests, in beach litter, meadows, pastures, prairies, sagebrush, and under logs and rocks.

Anyphaena furva was described by Miller (1967) from one male collected on a rock wall in the Zádielská Dolina valley, Slovakia. Šmaha (1985) collected one male in a scree field under Týřovská Skála rock in Křivoklátsko Reserve. Our finding of three males on tree trunks at Nezabudické Skály coincides to the biology of the closely related *Anyphaena accentuata* (Walckenaer 1802), and suggests that *Anyphaena furva* inhabits tree trunks on sun-exposed rocks and can occasionally move onto such rocks.

Rock as a habitat of thermophilous spe-

cies.—The frequency of specimens of thermophilous species amounts 43% at Nezabudické Skály, and 38% at Kotýz. Together, 26 thermophilous species belonging to 11 families were recorded.

The surface of sand dunes and scree slopes can be heated to high temperatures. This effect is caused by isolating air interlayers. The specificity of arachnofauna of sand dunes is well known. In contrast, we found no specific inhabitants of upper overheated margins of boulder accumulations. This is probably the result of the very low humidity of these sites (Růžička et al. 1995). Rocks are the third bare, natural habitat, which can also overheat.

Potential surface temperature and heat accumulation capacity are considered as the most important characteristics of thermal behavior of rocks. Different values of physical constants of particular rocks actually suggest that the rocky substratum may play a decisive role in the thermal balance of habitats dominated by larger exposed rock. Both andezite and limestone are considered to be "warm, calorific" rock with a predisposition to harboring isolated populations of thermophilous plant and animal species (Rejmánek 1971).

Thermophilous *Segestria bavarica* inhabits rocky habitats (in Switzerland and Austria), and also forests, where it was collected in pitfall traps and by hand-picking under bark (Noflatscher 1991; Maurer & Hänggi 1990). In the Czech Republic, it occurs exclusively on rocks. This case supports a hypothesis that, in some northern locations, thermophilous species narrow their ecological niche exclusively to south-exposed rocky habitats, and they can reach the northernmost range of their distribution in these habitats. For example, Jonsson (1995) recorded the most northern occurrence of several thermophilous species in Sweden on rocky habitats.

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RESEARCH NOTE

ANYPHAENIDAE IN MIOCENE DOMINICAN REPUBLIC AMBER (ARACHNIDA, ARANEAE)

Keywords: Anyphaenidae, Miocene amber, Dominican Republic

Anyphaenids have a worldwide distribution but are particularly common in the neotropics. They are medium to large, long-legged spiders with claw tufts formed from several rows of lamelliform setae, and the tracheal spiracle situated considerably more anteriorly than in other spiders; however, the latter character varies between genera. The family contains fast, active hunters, usually found on vegetation, particularly tree foliage.

In a revision of North American anyphaenid genera Platnick (1974) stated that the taxonomy of the approximately 375 Neotropical species was unclear. In a phylogenetic study, Ramírez (1995) established three anyphaenid subfamilies (Malenellinae Ramírez 1995, Anyphaeninae Bertkau 1878, Amaurobioidinae Hickman 1949), but considered the interfamilial relationships unclear. The subfamilies were delimited by the position of the tracheal spiracle, the structure of the tegulum and median haematodocha, and the structure of the female palpal tarsus.

Recent papers (Brescovit 1996 and references therein) have delimited many of the Recent Neotropical anyphaenid genera. Brescovit (1996) revised the Neotropical Anyphaeninae at the generic level, creating 14 new genera (new total 32), 12 new synonymies, and 70 new combinations. This paper newly combines the amber species *Anyphaeniodes bulla* (Wunderlich 1988) (= *Aysha bulla*) and *Lupettiana ligula* (Wunderlich 1988) (= *Teudis ligula*) in the light of Brescovit's (1996) revision (which omitted fossil taxa).

The Miocene Dominican Republic amber specimens studied, which are the only known representatives of the species concerned, were obtained from the Senckenberg Museum,

Frankfurt (SMF, courtesy of Dr. M. Graßhoff). This amber is considered to be approximately 15–20 million years old (Iturralde-Vinent & MacPhee 1996).

Anyphaenoides bulla (Wunderlich 1988)
new combination
Fig. 1

Aysha bulla Wunderlich 1988: 220, figs. 599–602, 764, holotype and only known specimen: male, SMF 38160, in Miocene Dominican Republic amber, examined.

Emended diagnosis.—Males of *A. bulla* can be recognized by the following combination of characters: embolus long, not forming a broad subcircular loop in the distal half of the cymbium, lacking a median constriction and a basal embolic process; large hook-shaped median apophysis with a broad base; tibia long with a simple retrolateral tibial apophysis. Female unknown.

Remarks.—This species can be excluded from *Aysha* Keyserling 1891 by having a simple palpal tibia (Wunderlich 1988: fig. 602) lacking complicated apophyses (e.g., Brescovit 1996: fig. 259).

Lupettiana ligula (Wunderlich 1988)
new combination
Fig. 2

Teudis ligula Wunderlich 1988: 221, figs. 603–605, 765, holotype and only known specimen: male, SMF 38152, in Miocene Dominican Republic amber, examined.

Emended diagnosis.—Males of *L. ligula* can be recognized by the following combination of characters: embolus (or conductor—see remarks) long, projecting ventrally; ventral tegular projection with pointed tip; retro-

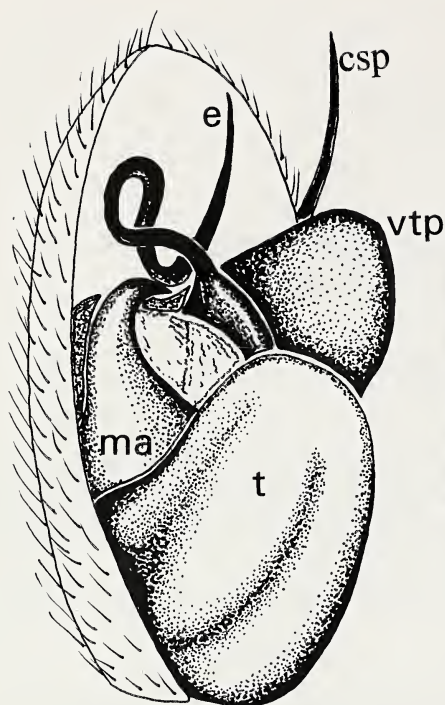


Figure 1.—Right pedipalp of *Anyphaenoides bul-la* new combination, male holotype, SMF 38160. Scale = 0.2 mm. Abbreviations: csp = cymbial spine, e = embolus, ma = median apophysis, t = tegulum, vtp = ventral tegular projection.

lateral tibial apophysis long, with rounded apex; palpal tibia without dorsal cusps. Female unknown.

Remarks.—In this specimen not all the palpal sclerites are visible because of the position in which the spider is preserved. The only view of the sclerites possible is that shown in Fig. 2, and it is not clear whether the anterior projection is the embolus or the conductor. However, the structure of the retrolateral tibial apophysis (Fig. 2; Wunderlich 1988: figs. 604–605) is a synapomorphy of the genus and is sufficient evidence for the proposed new combination. Eskov (1990) has commented that the amber spider fauna is taxonomically subequal to Recent faunas, and the certainty with which pattern-based species can be recognized in the fossil record is less than that for extant organisms (Smith 1994). This species can be excluded from *Teudis* O.P.-Cambridge 1896 by having a palpal tibia lacking short conical projections (e.g., Brescovit 1996: fig. 68).

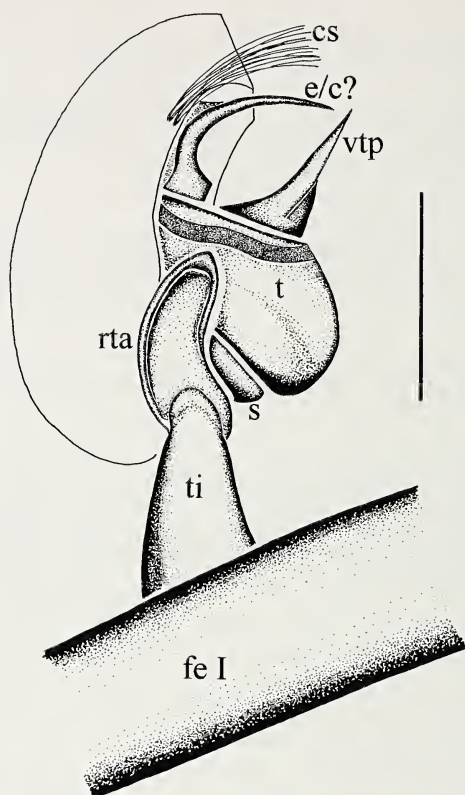


Figure 2.—Right pedipalp of *Lupettiana ligula* new combination, male holotype, SMF 38152. Scale = 0.2 mm. Abbreviations: cs = cymbial setae, e/c? = embolus or conductor (see remarks under *L. ligula*), fe I = femur I, rta = retrolateral tibial apophysis, s = subtegulum, t = tegulum, ti = palpal tibia, vtp = ventral tegular projection.

Wulfila spinipes Wunderlich 1988

Wulfila spinipes Wunderlich 1988: 218, figs 589–598, 762–763, holotype male SMF 38136, and one male paratype, SMF 38144, both in Miocene Dominican Republic amber, examined.

Remarks.—*Wulfila* as currently delimited contains approximately 40 species with Nearctic and Neotropical distributions (Brescovit 1996). The interspecific relationships are unclear and the genus is in need of revision. The specimens described by Wunderlich are retained in *Wulfila* due to the structure of the complicated retrolateral tibial apophysis, the long ventral tegular projection and the conical ventral coxal projections. Unfortunately, legs I are missing in both holotype and paratype, so it is impossible to determine their lengths relative to legs II; however, the specimens do not possess the large and distinct ventral che-

lateral tooth present in *Wulfilopsis* (e.g., Brescovit 1996: fig. 34). Wunderlich's diagnosis serves only to separate this species from the other described Dominican Republic amber spiders, and is not sufficient to separate it from all the extant *Wulfila* species. An emended diagnosis will have to wait, pending revision of the extant species or, preferably, the amber specimen would be included in such a revision.

DISCUSSION

These are the first fossil records of the genera *Anyphaenoides* and *Lupettiana*, taking them back 15–20 million years. As a result of the new combinations, *Aysha* and *Teudis* are not known in the fossil record.

Lupettiana is represented on Hispaniola by two, and *Wulfila* by three extant species, whereas *Anyphaenoides* is not recorded from the Recent Hispaniolan fauna (Penney 1999a). Brescovit's (1992) revision of the genus extended the known geographical range of *Anyphaenoides* from Peru, Ecuador and the Galápagos Archipelago, to include Panama, Venezuela, Surinam, Brazil and northern Argentina. Baert (1995) added Cocos Island in the Pacific. Hispaniola is unique in terms of its known spider fauna in that more families are recorded from fossil species in amber than are known from extant species (Wunderlich 1988; Penney 1999b). There have been 291 Recent species in 155 genera and 40 families recorded from Hispaniola (e.g., Banks 1903; Bryant 1943, 1945, 1948; Penney 1999a), but this fauna has not been intensively investigated using a variety of collecting techniques.

Evidence from sedimentary and geomorphic data, alluvial terraces and albedo reflectivity indices suggest that the Dominican Republic was not drastically affected by the Pleistocene glaciations (Schubert 1988), and the Tertiary Hispaniolan spider lineages have probably suffered no major habitat disruption that would cause their extinction. This is supported by the high degree of similarity between the species composition of the known Tertiary fauna and the Recent fauna (Penney 1999b). *Anyphaenoides* is recorded from the amber and is a component of the Recent Neotropical fauna; it can be predicted that this genus has at least one undiscovered Recent species present on Hispaniola.

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RESEARCH NOTE

EREMOPUS ACUITLAPANENSIS, A NEW SPECIES (SOLIFUGAE, EREMOBATIDAE, EREMOBATINAE) FROM GUERRERO, MÉXICO

Keywords: Solifugae, Guerrero, Mexico

A medium-to-deep fondal notch is usually present below the fixed finger on the chelicerae of male eremobatine solifugids. While studying a series of these arachnids from Guerrero, México, collected by members of the Instituto de Biología of Universidad Nacional Autónoma de México, we discovered a new eremobatine species whose uniquely modified fixed cheliceral finger bears a mesoventral flange that covers the fondal notch. Vázquez (1986) illustrated this species, but he did not offer a formal description. We now present a description.

Nomenclature and measurements (mm) were made as described in Muma (1951). The ratios CL/CW, PW/PL and A/CP, as defined by Brookhart & Muma (1981) and ECCS setae are also provided. Colors are from specimens preserved in alcohol. Type depositories are abbreviated as follows: IBUNAM = Laboratorio de Acarología, Instituto de Biología, Universidad Nacional Autónoma de México, Coyoacán 04510, D.F., México; AMNH = American Museum of Natural History, New York.

Eremopus acuitlapanensis new species
Figs. 1–9, Tables 1, 2

Types.—Holotype, male: Mexico: *Guerrero*: Acuitlapan, 25 km East of Taxco (17°35'N, 99°15'W), 13 October 1976, Melgar, Novelo, Chavarría, collectors. Deposited in IBUNAM. Paratypes: Mexico: *Guerrero*: Acuitlapan, 13 October 1976, Melgar, Novelo, Chavarría, 1♂ (IBUNAM); Las Granadas, 28 October 1980, [collector unknown], 1♂ (AMNH); Acuitlapan, 25 km east of Taxco (17°35'N, 99°15'W), 13 October 1976, E. Cer-

vantes, 1♀ (IBUNAM); Acuitlapan, 23 January 1978, I. Espejel, 1♀ (AMNH).

Etymology.—The species name *acuitlapanensis* refers to Acuitlapan, Guerrero state, México, the place where the specimens were collected.

Diagnosis.—The presence on males of a wide, shallow, almost indistinct mesal crease on the fixed cheliceral finger, an anterior tooth on the movable cheliceral finger, and four long, stout needle-like ctenidia on the first post-spiracular abdominal sternite suggest a close relationship of this species to *Eremopus montezuma* Roewer 1934 and *Eremopus fuscus* (Muma 1987). Males of *Eremopus acuitlapanensis* new species are easily distinguished from other members of the genus by the presence of a mesoventral flange on the basal one-third of the fixed cheliceral finger. The flange almost covers the entire fondal notch. The genital opercula of females of *Eremopus acuitlapanensis* new species are similar to those of *E. fuscus* females, but the lateral concavities of *E. acuitlapanensis* opercula are a little closer together and the posterior margins are well-defined.

Description.—*Male*: Propeltidium yellow, wider than long, with a narrow, dusky band on anterior margin (measurements in Table 1). Eye tubercle dark; eyes separated by almost two diameters. Dorsal opisthosoma dark brown-to-black with pleural membranes grey-to-brown. First post-spiracular abdominal sternite provided with four long, stout needle-like ctenidia (Fig. 6), these extending beyond the middle of the succeeding sternite. Chelicera (Figs. 1–5) robust, yellow; dentition reddish-brown. Fixed finger straight, slightly down-

Table 1.—Measurements (mm) of male holotype and male paratypes of *Eremopus acuitlapanensis*. The data are taken from the holotype and two paratype specimens.

Structure	Length		Width		Ratios	
	Holotype	Paratype	Holotype	Paratype	Holotype	Paratype
Chelicerae	7.5	7.5, 7.7	3.7	3.7, 3.7	CL/CW = 2.03	2.03, 2.08
Propeltidium	4.0	4.0, 4.0	5.5	5.5, 5.7	PW/PL = 1.37	1.37, 1.42
Palpi	22.2	21.5, 22.2			A/CP = 6.09	5.83, 5.79
Legs I	18.4	18.0, 16.5				
Legs IV	29.5	27.5, 29.0				

turned distally, with part of the basal one-third forming a mesoventrally directed flange that covers almost the entire fondal notch (see arrow in Fig. 3). Mesal surface of fixed finger with a wide, shallow, crease extending from the tip of the finger a point above the uppermost tooth (I) of the ectal fondal tooth row (Fig. 3). Fondal teeth arranged in two rows of four teeth each, both graded I, III, II, IV in size. Movable finger with low, flattened anterior tooth, large principal tooth, and two small intermediate teeth contiguous with the principal tooth; small, distinct mesal tooth present. Flagellum complex with dorsal series of simple tubular setae and ventral series of slightly striate to plumose setae. Apical bristles of flagellum complex not conspicuously enlarged or flattened. Ectal cheliceral cluster setae as in Fig. 5. Palpi yellow, each with many cylindrical spine-like setae and long whip-like setae; scopula absent. Legs yellow, without dark markings. Malleoli white.

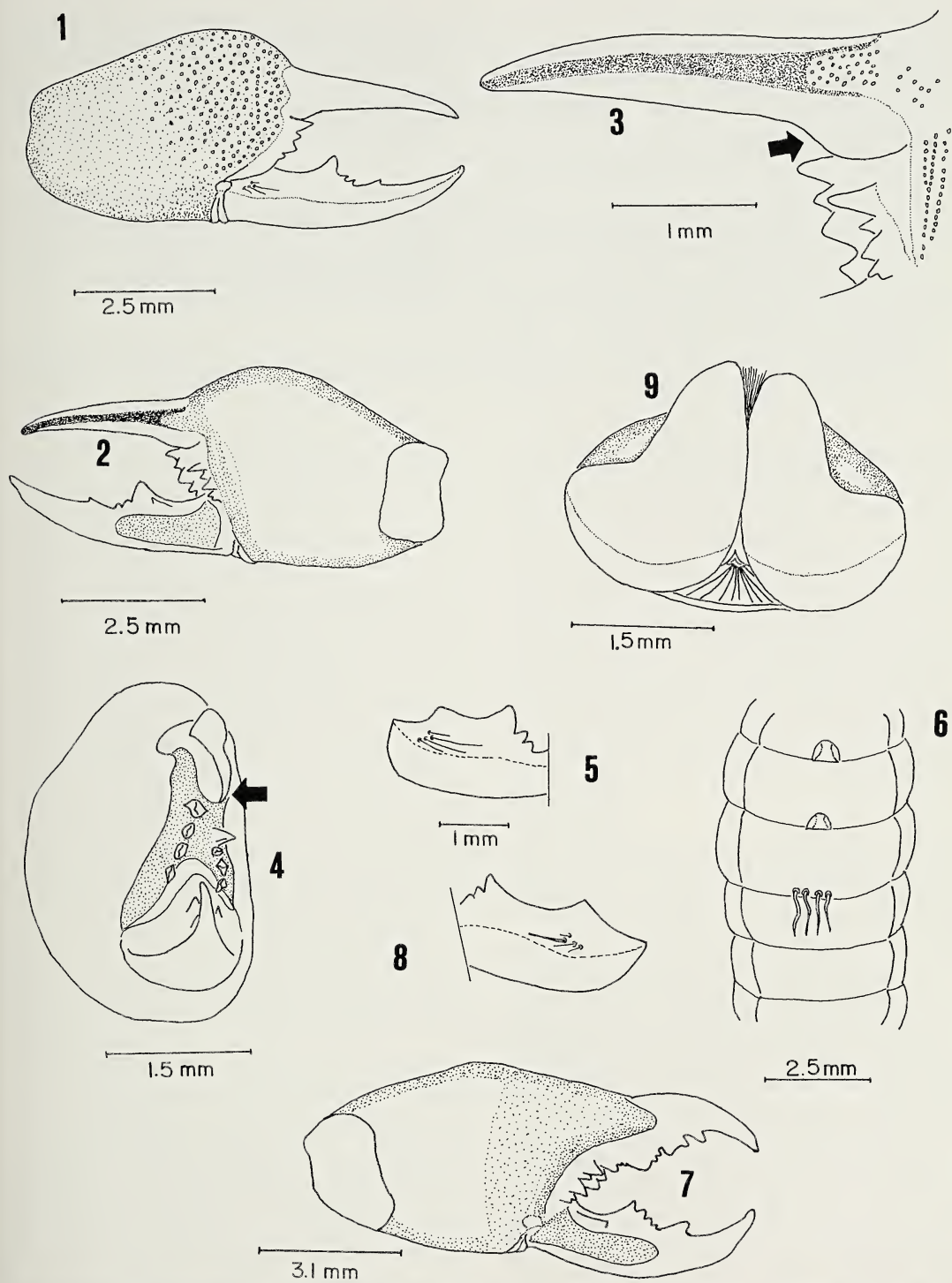
Female: Similar in form and coloration to male, but differing as follows. Opercula of genital segment (Fig. 9) with lobes extended laterally, slightly separated anteriorly and posteriorly, with a well-defined posterior border, and with a concavity on the ectal side of each

lobe. First post-spiracular sternite without ctenidia. Chelicerae (Fig. 7) proportionally larger than those of male. Fixed finger with a large principal tooth, a slightly smaller medial tooth, an anterior tooth which is half the size of the principal tooth, a well-developed intermediate tooth between the anterior and medial teeth, and three small intermediate teeth contiguous with the anterior margin of the principal tooth. Movable finger with a large principal tooth, a well-developed anterior tooth, and three small intermediate teeth contiguous with the anterior margin of the principal tooth; small, distinct mesal tooth present. Ectal cheliceral cluster setae as in Fig. 8.

This contribution is dedicated to the memory of Dr. Leonila Vázquez García, Curator of Arachnology, Instituto de Biología (IBUN-AM), for providing us with facilities in which to study the museum's specimens. Thanks also to Dr. Anita Hoffmann, Laboratorio de Acarología "Anita Hoffmann," Facultad de Ciencias, UNAM, for the opportunity to work with her arachnological collection deposited at IBUNAM. We are also grateful to Dr. Warren E. Savary for his critical review of the manuscript.

Table 2.—Measurements (mm) of female paratypes of *Eremopus acuitlapanensis*; the museum acronyms are given.

Structure	Length		Width		Ratios	
	IBUNAM	AMNH	IBUNAM	AMNH	IBUNAM	AMNH
Chelicerae	9.5	10.0	4.0	4.0	CL/CW = 2.40	2.50
Propeltidium	4.0	4.5	7.0	7.0	PW/PL = 1.75	1.55
Palpi	20.0	20.0			A/CP = 4.44	4.55
Legs I	16.0	17.0				
Legs IV	24.0	29.0				



Figures 1–9.—*Eremopus acuitlapanensis* new species. 1–6, Male holotype. 1. Ectal view of right chelicera; 2. Mesal view of right chelicera; 3. Mesal view of right chelicera (detail); 4. Frontal view of right chelicera; 5. Holotype ECCS setae of right chelicera; 6. Ventral view of abdominal ctenidia. 7–9. Female paratype. 7. Mesal view of left chelicera; 8. ECCS setae of left chelicera; 9. Genital opercula.

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RESEARCH NOTE

EXTERNAL MORPHOLOGY AND ULTRASTRUCTURE OF THE PREHENSILE REGION OF THE LEGS OF *LEIOBUNUM NIGRIPES* (ARACHNIDA, OPILIONES)

Keywords: Chemoreception, harvestmen, locomotion, setae

Species of harvestmen (Arachnida, Opiliones, Palpatores) in the family Sclerosomatidae frequently employ prehensile flexion of the telotarsus during locomotion. Kaestner (1968) described the ability of these arachnids to anchor themselves to objects such as blades of grass by wrapping their legs around these objects. We have observed both *Leiobunum nigripes* (Weed 1892) and *L. vittatum* (Say 1821) moving across surfaces by forming coils at the end of their legs, especially the second pair (Figs. 1–4). While moving across a smooth substrate, these harvestmen cast the coiled regions of their legs about until they catch on a structure. Similar strategies are also employed by harvestmen during climbing, with the exception being that once a purchase is obtained with a coil, the legs often wrap around and climb up the anchored leg. In addition, we have also observed harvestmen in aggregations wrapping their legs around the legs of adjacent individuals (Fig. 2).

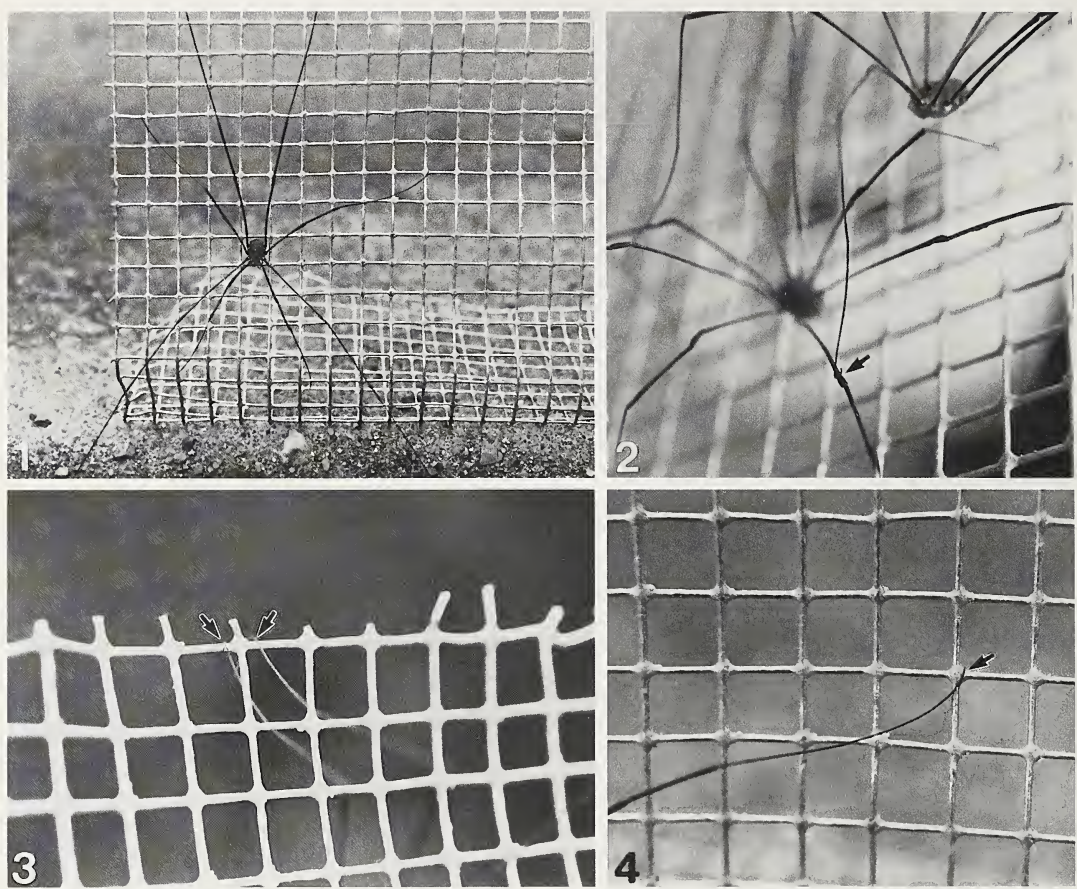
Movement of the legs in harvestmen has been hypothesized to occur through a combination of muscle action and a hydraulic pump mechanism (Shultz 1989; Foelix 1996). According to this hypothesis, hemolymph is pumped into the legs by contraction of either the muscoli laterales or the endosternal muscles (the primitive condition: Shultz 1991) of the prosoma (Parry 1960), resulting in leg extension. For harvestmen, Shultz (1989) reported that the basitarsus and telotarsus of the

leg are traversed by two tendons arising from muscles that are used to move the tarsal claw. The telotarsus is subdivided by numerous adesmatic joints (>50: Kaestner 1968) that impart a prehensile character to the tarsus when flexed (Figs. 5–7). Flexion at the adesmatic joints can occur only ventrally in *L. rotundum* (Latreille 1795) because the ventral joint membranes are shorter than the dorsal joint membranes (Kaestner 1968). In this paper we describe the external morphology and ultrastructure of the prehensile region of the legs of juveniles of *Leiobunum nigripes* (Sclerosomatidae).

We collected juvenile *Leiobunum nigripes* from Chicot State Park, Evangeline Parish, Louisiana on 8 March 1997 and housed them in screened aquaria for approximately one week prior to preservation. Within 48 h after molting, specimens were fixed in cold (4 °C) Trump's fixative (a mixture of sodium cacodylate buffer, formalin, and glutaraldehyde) overnight, rinsed in 0.2 M sodium cacodylate buffer (pH = 7.4) and postfixed in 2% OsO₄ for 90 min at room temperature. Specimens were then dehydrated in a graded ethanol series and chemically dried with hexamethyldisilazane (Nation 1983), mounted on aluminum stubs, and sputter-coated for 2 min with ~20 nm of gold. We examined and photographed these specimens with a JEOL 6300-F field emission scanning electron microscope at accelerating voltages of 15–20 kV.

Specimens examined with transmission electron microscopy (TEM) were fixed and dehydrated using the same protocol described above for scanning electron microscopy

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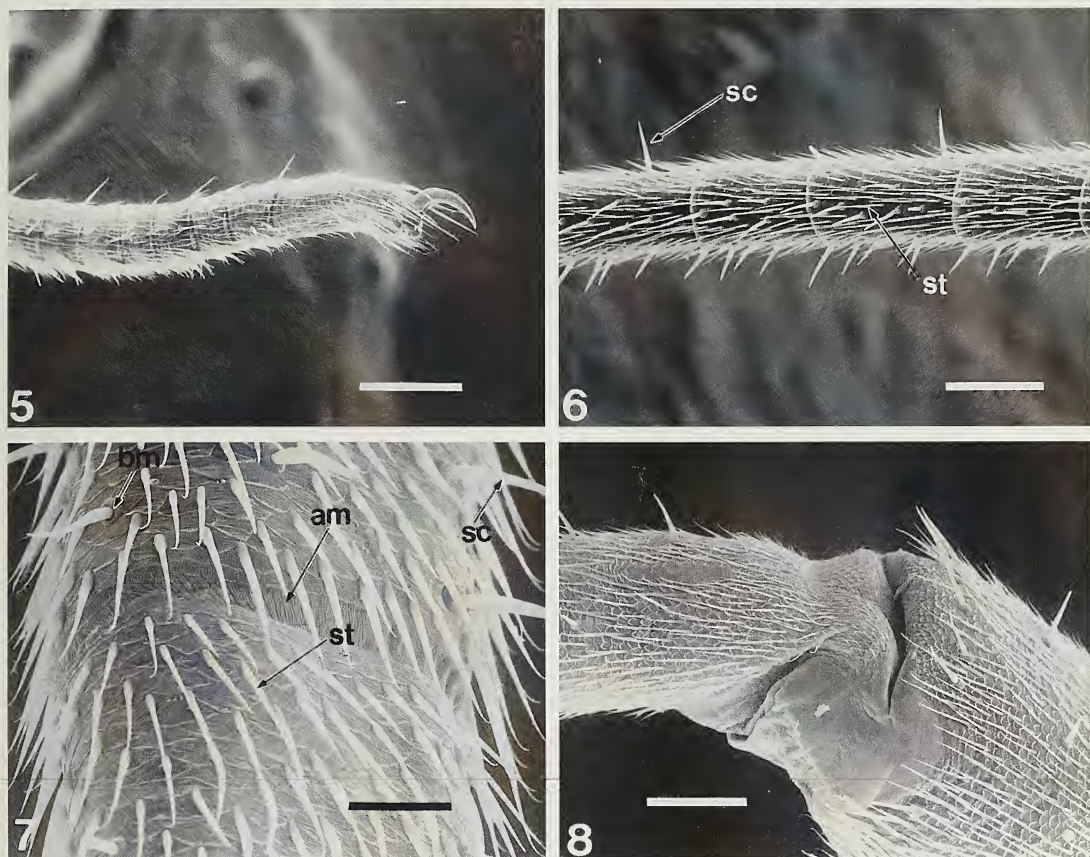
Figures 1–4.—Adults of the harvestman *Leiobunum nigripes* on hardware cloth (mesh size 6 mm × 6 mm) showing the prehensile ability of the tarsi. 1. An individual anchored to the substrate; 2. A small aggregation of harvestmen in which one individual has wrapped one of its leg around the leg of another; 3, 4. Dorsal views of the prehensile region of the tarsi, showing the wrapping of the legs around individual metal wires. Arrows in each figure indicate regions of flexion in the distal tips of the telotarsus.

(SEM). Following dehydration, specimens were slowly infiltrated in Spurr's low viscosity standard resin (Spurr 1969) over four days and sectioned with a diamond knife. Thin sections were collected on carbon-stabilized 200 μm thin bar grids, stained sequentially with methanolic uranyl acetate and aqueous lead citrate, and observed with a Hitachi H-7000 transmission electron microscope at 75 kV.

On each leg, *L. nigripes* has a single, smooth tarsal claw that is not toothed (Fig. 5). Smaller setae, or sensilla trichodea (Schneider 1964; Spicer 1987), and larger primary spines, or sensilla chaetica (Schneider 1964; Spicer 1987), are denser on the ventral surface of the telotarsus than on the dorsal surface (Fig. 6). The sensilla trichodea lie nearly parallel with the surface of the leg and have no specialized

basal articulating membrane (Figs. 6, 7). The sensilla chaetica are nearly perpendicular to the leg surface and have a specialized basal articulating membrane (Figs. 11, 12), with blunt tips and whorled striae (Fig. 14), unlike those of sensilla trichodea (Figs. 6, 7). There is no evidence of trichobothria, mechanoreceptors that are common to most arachnids (Reissland & Görner 1986; Foelix 1996). The adesmatic joints are easily distinguished from true joints (Fig. 8) on the basis of their small size.

Cross sections examined with TEM confirmed the earlier anatomical observations of Kaestner (1968); i.e., no muscles were found between the segments of the telotarsus (Fig. 9). We observed only a single tendon (Fig. 9) connecting the tarsal claw to the claw-flexing



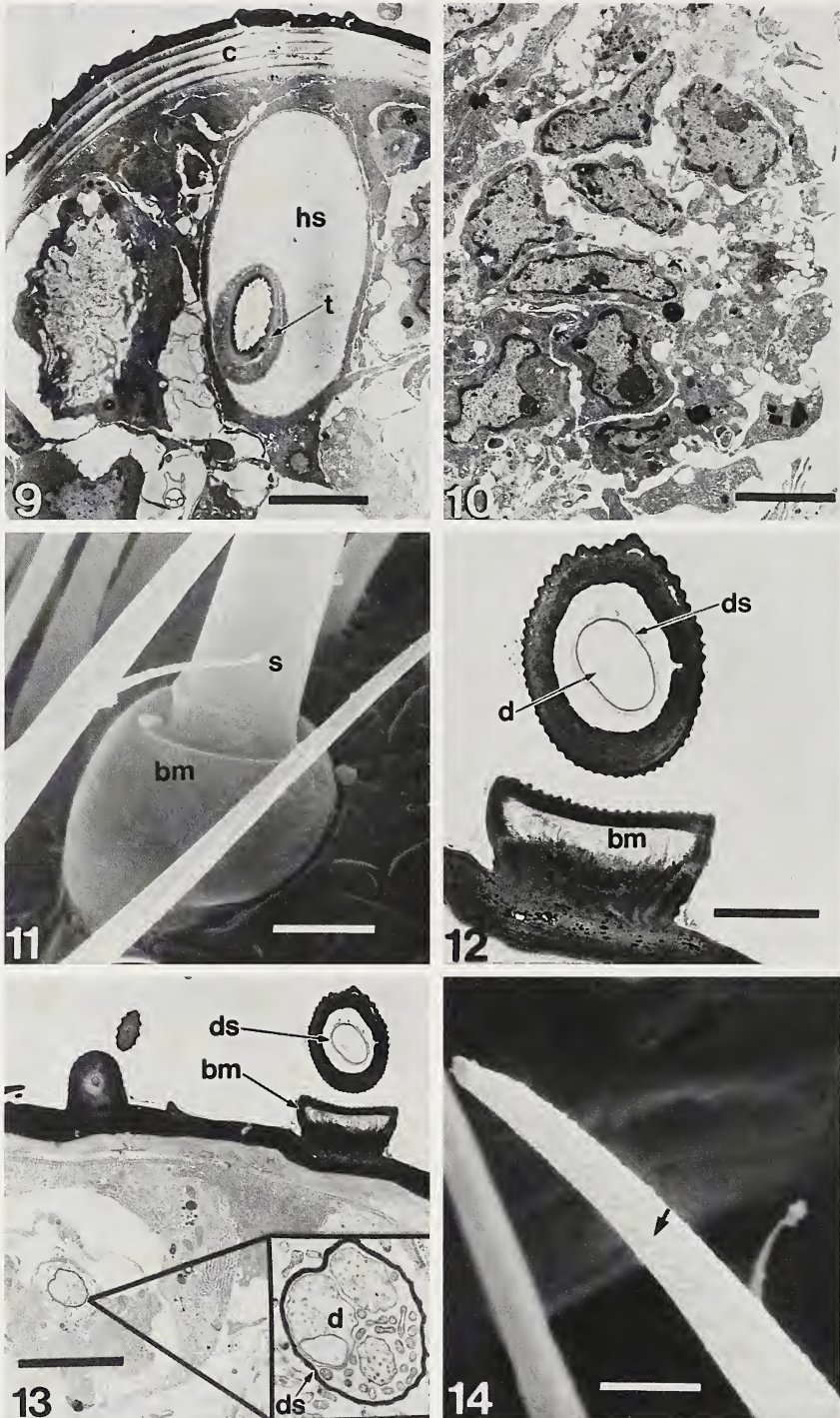
Figures 5–8.—External morphology of tarsus IV of *Leiobunum nigripes*. 5. Lateral view of the telotarsus and tarsal claw. Scale bar = 127 μm ; 6. The adesmatic joints on the ventral surface of the telotarsus. Scale bar = 64 μm ; 7. The sensilla trichodea (st) and sensilla chaetica (sc) on the ventral surface of the telotarsus near an adesmatic membrane (am) of an adesmatic joint. Scale bar = 23 μm ; 8. A lateral view of a true joint between the two most distal segments of a leg, the basitarsus and the telotarsus. Scale bar = 73 μm .

musculature located in the tibia. In the telotarsus, we also observed epidermal cells lining the innermost portions of the cuticle (hypodermis) and occurring in clusters within the leg hemocoel (Fig. 10).

During the course of our TEM studies of the internal features of the leg, several sections provided information concerning the innervation of the sensilla chaetica (Figs. 6, 7, 11). Apical pores, a common feature of sensilla chaetica among arthropod chemoreceptors (reviewed in Zacharuk 1980), were not observed in our specimens. This sensillum is innervated by many presumably chemoreceptive dendrites (Figs. 12, 13). The dendrites originate from enveloping cells within the hypodermis (Fig. 13; inset) which

do not attach to the cuticular wall of the basal articulating membrane. Instead, the sheath containing the dendrites passes directly through the center of the setal shaft (Fig. 12, 13), a common feature of arthropod chemoreceptors (Altner & Prillinger 1980; Zacharuk 1980).

The external morphology of the prehensile region of the legs of *Leiobunum nigripes* is similar to that reported by Kaestner (1968) for *L. rotundum* and by Holmberg & Cokendolpher (1997) for *Togwoteus biceps* (Thorell 1877). Our observations of the sensilla on the tarsi of *L. nigripes* are also similar to those reported by Spicer (1987) for the palps of *L. townsendi*. The most numerous sensory organs on the legs of *L. nigripes* appear to be



Figures 9–14.—Ultrastructure of the telotarsus of leg IV of *Leiobunum nigripes*. 9. TEM micrograph of a cross section of the telotarsus revealing a single tendon (t) within a hemocoelic space (hs) and showing no muscle or tendon attachments with the inner surface of the cuticle (c). Scale bar = 6 μ m; 10. TEM micrograph of the epidermal cells lining the innermost portion of the cuticle. Scale bar = 3 μ m; 11. SEM micrograph of the specialized basal articulating membrane (bm) of a sensilla chaetica (s) from the ventral surface of the telotarsus. Scale bar = 3 μ m; 12. TEM micrograph of a basal articulating membrane and shaft of a sensilla chaetica revealing the dendrites (d) and dendritic sheath (ds) within the shaft of the

sensilla chaetica (primary spines) and sensilla trichodea (setae). Unlike the palps of *L. townsendi*, however, these sensilla appear to be more numerous on the ventral surface of the telotarsus than the dorsal surface. Spicer (1987) also reported two types of sensilla chaetica (types I and II) based on the differing lengths of the sensilla. We observed only one type of sensilla chaetica in *L. nigripes*. We also did not observe any pores that are characteristic of chemoreceptors on the sensilla chaetica (Slifer 1970), but the structure of the dendrites innervating them (e.g., many dendrites and lack of attachment to the basal articulating membrane) indicates that they may function in chemoreception. Spicer (1987) inferred that the row of spines found on the ventral surface of the palps of *L. townsendi* were chemoreceptors and such receptors have been reported for other species of harvestmen (e.g., Foelix 1985).

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seta. Scale bar = 2 μ m; 13. TEM micrograph of a sensilla chaetica, the cuticle and the underlying structure within the telotarsus. The inset is of a nerve from a chemoreceptive setae, revealing multiple dendrites within a single dendritic sheath. Scale bar = 5 μ m; 14. SEM micrograph of the distal tip of a sensilla chaetica revealing the whorled striae on the external surface and the lack of a discernable pore at the tip. Scale bar = 3 μ m.

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RESEARCH NOTE

A COMPARATIVE STUDY OF SEXUAL BEHAVIOR IN TWO SYNMORPHIC SPECIES OF THE GENUS *LYCOSA* (ARANEAE, LYCOSIDAE) AND THEIR HYBRID PROGENY

Keywords: Spider hybrid courtship, hybrids, species-specific recognition

Lycosa thorelli Keyserling 1877 and *Lycosa carbonelli* Costa & Capocasale 1984 are syn-morphic, synchronic and sympatric species (Costa & Capocasale 1984) that, however, can be collected in different microhabitats (unpubl. data). Males are slightly different in their female-searching behavior, but differ clearly in their courtship in front of females, thus avoiding interbreeding (Costa & Capocasale 1984). Costa & Francescoli (1991), using anaesthetized females, obtained an exceptional hybrid brood (from *L. thorelli* male and *L. carbonelli* female) and two conspecific control broods. These three broods were raised to adulthood (Francescoli & Costa 1992) and then used in the present study.

Costa et al. (1997), analyzing the behavior of parental (*L. thorelli* and *L. carbonelli*) and hybrid males elicited by female hybrid pheromone, found that hybrid males showed an intermediate behavioral pattern between both parental species and a low activity level. Parental males showed an intermediate activity level when compared to the activity elicited by conspecific and heterospecific stimuli.

In this paper, we analyzed (1) the behavior of the above mentioned males elicited by the parental species' sexual pheromone, and (2) the direct interactions among the males and the females of the three groups. This study allows a thorough comparison of the sexual behavior of the three groups released by different sexual stimuli. Also, these data facilitate both a deeper analysis of the function of reproductive isolation mechanisms and the formulation of hypotheses about signal effectiveness, mechanisms of heritability, and the possible evolutionary paths taken by the courtship behavior of these species.

We used 5♂ and 2♀ *L. thorelli*, 8♂ and 3♀ *L. carbonelli*, and 9♂ and 8♀ hybrids. Also, one wild-caught female *L. thorelli* and one

wild-caught *L. carbonelli* were used as sex pheromone donors. Spiders were housed in the same conditions as in Costa et al. (1997). Voucher specimens were deposited in the entomological collection of the Facultad de Ciencias, Montevideo.

During the experiments the females were kept in glass containers (15 cm diameter × 5 cm high) with sand as a substrate. Two types of experiments were done. Males were observed in: (1) the presence of one parental sex pheromone, and (2) in the presence of both the female spider and the corresponding sex pheromone. In the first type, the females remained in the containers at least 24 h and were taken out immediately before the introduction of the male. The male was gently introduced, and his behavior was observed for 5 minutes. In the second type, we introduced a female at least 24 h before the experiment and the behavior of the male was then recorded after visual or tactile contact with the female. To reduce the probability of attacks, the male was introduced behind an opaque barrier. Experiments were ended when: (1) the male performed 60 minutes of sexual activity without copulation; (2) no sexual behavior was observed for 20 minutes; (3) copulation was completed; (4) the female attacked the male. Room temperature during the experiments was $23.4 \pm 1.5^\circ\text{C}$.

Forty-three trials were done, 15 in the context of female sex pheromone only and 28 in the context of the female and sex pheromone. The trials with pheromone only were (H = hybrids, C = *L. carbonelli*, T = *L. thorelli*; the first letter corresponds to the male and the second to the female): HC (4 trials), CC (2), TC (2), CT (2), TT (2), HT (3); data from HH, CH and TH were taken from Costa et al. (1997). The trials with females were: HH (5 trials), HC (3), HT (3), CH (3), CC (3), CT

Table 1.—Single records of rhythms and angles for leg movements. Data taken only from videos that allowed clear, on-screen measurements. Rhythms measured in movements/second; angles covered by leg movements measured in degrees. Groups were identified with two letters, the first corresponding to the male species and the second corresponding to the female (or pheromone donor): H = hybrids, C = *L. carbonelli*, T = *L. thorelli*. “—” denotes no data.

Behavior	Experimental group			
	HC	CC	CT	TT
Leg waving				
Rhythm	8.2	3.6	3.5	—
Angle	13.8	22.9	21.3	—
Rubbing				
Rhythm	—	—	—	11.8
Drumming				
Rhythm	7.0	4.0	5.0	4.6
Leg tapping				
Rhythm	—	2.7	3.3	—
Angle	—	28.0	25.1	—

(2), TH (3), TC (3) and TT (3). Individuals were used randomly, avoiding consecutive trials for the same individual. The low number of observations was because of the extremely limited number of available individuals (Francescoli & Costa 1992) and the risk involved in direct sexual encounters. The trials were video-taped and analyzed using 19 behaviors. Some behaviors are composed by more than one act that occur simultaneously. The behaviors observed in this study were: Abdominal vibrations (AV), Attack (At), Copulation (Co), Drumming (Dr), Explosive locomotion (EL), Immobility (Im), Leg tapping (LT), Leg waving (LW), Locomotion (Lo), Locomotion-with-Drumming (Lo/Dr), Locomotion-with-Leg tapping (Lo/LT), Locomotion-with-Leg waving (Lo/LW), Locomotion-with-Leg waving-with-Drumming (Lo/LW/Dr), Locomotion-with-Palpatation (Lo/Pa), Locomotion-with-Palpatation-with-Leg tapping (Lo/Pa/LT), Palpatation (Pa), Positioning (Po), Rest posture (RP) and Rubbing of legs (Ru).

Comparisons using data obtained here and data from Costa et al. (1997) were made. The mean repertoire size comparisons used both sexual behaviors and all behaviors. Mean repertoire size was the average number of differ-

Table 2.—Repertoire size in experimental groups responding to parental pheromone. “—” denotes no data. HH, CH and TH data were taken from Costa et al. (1997).

Group	Reper- toire size	Num- ber of obser- vations	Repertoire size values as X̄ (SD)	
			All units	Sexual units
HH	21	46	5.80 (3.59)	3.78 (3.19)
CH	19	16	7.90 (3.20)	5.69 (3.28)
TH	22	15	8.13 (5.59)	6.07 (5.26)
HC	6	4	2.75 (2.22)	1.00 (2.00)
CC	6	2	3.00 (1.41)	2.00 (0.00)
TC	1	2	1.00 (0.00)	—
HT	5	3	2.33 (1.53)	1.33 (1.53)
CT	8	2	5.00 (1.41)	2.00 (2.83)
TT	9	2	5.00 (4.24)	3.00 (4.24)

ent behaviors presented in any experiment for each group. Single measurements of rhythms and angles for leg movements in some behaviors were obtained (Table 1).

The repertoire sizes of males stimulated by parental sex pheromone were smaller in relation to those elicited by hybrid pheromone (Table 2). Comparisons of mean repertoire size for the same kind of male and for the same kind of pheromone were made. In the first comparisons, HH was significantly different than HT ($t = 3.37, 0.01 > P > 0.001$) and than HC ($t = 2.48, 0.02 > P > 0.01$), using all behaviors. Using sexual behaviors, HH was different from HT ($t = 2.45, 0.02 > P > 0.01$) and from HC ($t = 2.52, 0.02 > P > 0.01$). TH showed the biggest mean repertoire size and TC showed the smallest one (all behaviors; $t = 4.94, P < 0.001$). CH was significantly different than CC (all behaviors: $t = 3.0, 0.01 > P > 0.001$; sexual behaviors: $t = 4.5, P < 0.001$).

In the second type of comparisons, HH was significantly different than CH (all behaviors: $t = 2.19, 0.05 > P > 0.02$; sexual behaviors: $t = 2.02, 0.05 > P > 0.02$). In the intraspecific trials, sexual behaviors such as Leg waving, Drumming and Rubbing (and Explosive locomotion in *L. thorelli* male) were usually performed. In the interspecific trials only *L. carbonelli* males performed some sexual behaviors. Hybrid males performed Leg waving, Drumming, Palpatation and Leg tapping as sexual behaviors in the presence of parental sexual pheromones.

Table 3.—Some behaviors observed in direct male-female encounters. Only presence of each unit in the experiences are listed. No sex = absence of sexual behavior. Experimental groups identified as in Table 1. Behavior abbreviations are LW = leg waving, Ru = rubbing of legs, Dr = drumming, AV = abdominal vibrations, EL = explosive locomotion, RP = rest posture, At = attack. One experiment of the CT group was deleted due to the absence of sexual behavior during the 20 minute period.

Group (n)	No sex	Male					Female				
		LW	Ru	Dr	AV	EL	LW	Dr	RP	At	Copulation
HH (5)	0	4	2	4	1	0	0	0	0	4	0
HC (3)	2	1	1	1	1	0	1	1	1	2	0
HT (3)	1	2	1	1	0	0	1	0	1	2	0
CH (3)	2	0	0	1	0	0	0	0	0	2	0
CC (3)	0	3	1	3	1	0	1	1	1	2	1
CT (2)	2	0	0	0	0	0	0	0	0	1	0
TH (3)	1	1	0	1	0	0	0	0	0	2	0
TC (3)	1	0	0	2	0	0	0	0	0	2	0
TT (3)	0	3	0	1	1	3	0	0	0	1	1

Data for male-female encounters are showed in Table 3. In one HC experiment, the male performed four unsuccessful mount attempts.

Our results suggest that Leg waving, Drumming and Rubbing may be essential visual and acoustic signals for species recognition. These behaviors had constant species-typical characteristics (rhythms and angles) even when exposed to different pheromones. Parental females would discriminate slight differences in movement frequencies and angles from the signalling males. In *Lycosa malitiosa* Tullgren 1905, for example, the males were not recognized by conspecific females when the sexual signalling frequencies were experimentally changed (Costa & Sotelo 1983). Taking into account the complete precopulatory isolation between *L. thorelli* and *L. carbonelli* (Costa & Capocasale 1984), the absence of recognition of hybrid males by parental females was expected. However, the intermediate characteristic of the hybrid male signals elicited less intense rejections by parental females than the heterospecific males.

In the present study males showed a narrower repertoire than when exposed to hybrid pheromone (Costa et al. 1997) in both sexual and all behaviors. The absence of palpation in all its forms in males exposed to parental pheromones is remarkable, because of its occurrence in the presence of hybrid pheromone (Costa et al. 1997). This fact could be explained assuming that the hybrid pheromone is composed of species-specific tachochemical elements from both parental species, then in-

creasing the male repertoires. In agreement with Costa & Capocasale (1984), *L. carbonelli* and *L. thorelli* males showed a poor repertoire when tested with the heterospecific pheromone. The absence of reaction in males in the two TC cases also supports this view.

In direct male-female encounters, male *L. carbonelli* were best at discriminating, because they displayed low sexual activity in response to *L. thorelli* and hybrid females (Table 3). This is in agreement with the results reported by Costa & Francescoli (1991) using anesthetized females. Hybrid males were the least discriminating, but they did not succeed in obtaining copulation.

The low attack level in female *L. thorelli* could be considered as indicative of sexual receptivity. The low level of sexual displaying in female *L. thorelli* does not indicate non-receptivity because these females are usually passive (Costa & Capocasale 1984). Our results show the absence of receptivity in hybrid females tested with the three types of males, and in parental females tested with heterospecific males. Stratton & Uetz (1986) reported similar responses in hybrid females of *Schizocosa ocreata* and *S. rovneri*, and rejection of hybrid males by parental females. The moderate tolerance of parental females to hybrid males would be based on the presence of some elements from both parental courtship behaviors.

The occurrence of copulations in conspecific experimental groups indicates that the laboratory conditions did not affect sexual communication. Thus, the absence of copu-

lations in the other groups suggests that natural hybrids—if they occur—will not reproduce. However, a *L. carbonelli* female received an intense courtship and repeated mounting attempts from one hybrid male. This female was receptive probably due to the recognition of some species-specific signals; but, at the mounting attempt, she could have detected chemotactile information from the males' integument, allowing rejection.

The characteristics of both parental species' courtship displays agree with the hypothesis from Bristowe & Locket (1926) on the origin of those displays by ritualization of searching movements. Furthermore, both species show similar behaviors when exposed to sex pheromone, but in presence of conspecific females, *L. thorelli* males change their behavior while *L. carbonelli* males maintain the searching pattern (Costa & Capocasale 1984). The common ancestor would have had a similar pattern to that of *L. carbonelli* because the pattern is performed in the searching phase by both species.

Although sympatric, *L. thorelli* are captured mainly in sunny short-grass areas, whereas *L. carbonelli* are captured in tall-grass areas, including dark and humid places. The Explosive locomotion performed by a *L. thorelli* male would only be seen in open areas. *L. carbonelli* shows a pattern fitted to dark and closed areas with multiple obstacles, consisting of "cautious" locomotion, and a high occurrence of Leg waving using their long legs. These two different habitats may have determined the distinctive characteristics of the observed courtship patterns.

The precopulatory isolation between *L. thorelli* and *L. carbonelli* could have evolved by a process of alteration in the communication codes, from a mutation or recombination of the genes responsible of the signalling frequency. Indeed, movement frequencies during some displays were greater in *L. thorelli* than *L. carbonelli* (Costa et al. 1997). Also, Explosive locomotion could have originated by a Lo/LW frequency increase alternating with prolonged immobility periods. In this process the well-known high selectivity level of the female should play the main role (Suwa 1985). Stratton & Uetz (1986) suggested that *Schizocosa ocreata* and *S. royneri* speciated by alterations in the courtship pattern of their ancestor. In those species these authors postulated a model involving a mutation in "single autosomal

loci." Results from *L. thorelli* and *L. carbonelli* suggest that more complex genetic determination mechanisms are involved.

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RESEARCH NOTE

ESTIMATING FORAGING INTAKE: A COMMENT ON TSO AND SEVERINGHAUS (1998)

Keywords: Energy intake, allometry, digestible biomass

Tso & Severinghaus (1998) have recently drawn attention to the problems of using Schoener's (1980) length-weight equations for insects as a means of estimating foraging intake by spiders. They pointed out that a biomass estimate calculated from Schoener's equations includes all tissues irrespective of whether they are digestible or not. As predators do not utilize largely indigestible material (e.g., the exoskeleton—but note that at least some spider species can produce chitinase (Collatz 1987)) this will inevitably lead to inaccuracies in determining digestible biomass acquisition by a foraging spider. Tso & Severinghaus (1998) therefore measured the actual biomass removed from a variety of prey items of different sizes and taxonomic groups by caged female *Argiope trifasciata* (Forskål 1775). They did this by simply subtracting the weight of the discarded exoskeleton from the initial wet weight of the prey. Dry weights of the prey items used were estimated by inserting prey lengths into Schoener's (1980) equations for each of the various taxonomic groups. Plots of ingested biomass and of dry weights of prey against prey length yielded curves that increasingly diverged towards higher prey lengths. Tso & Severinghaus assume dry weight is composed of digestible biomass + exoskeleton; ingested biomass is composed of digestible biomass + water; the relative proportions of these three components are constant and the absolute contribution of each is a function of size. This being so, because water comprises a large proportion of the wet weight (and therefore, ingested biomass) the absolute difference between ingested biomass and dry weight will be a positive function of size—the plotted curves will di-

verge with increasing body length. The conclusion is that because many large spiders take a great range of prey sizes "... the relative energy content of large prey would be greatly underestimated if determined by dry weight alone." They recommend that "future studies should consider using ingestible biomass of prey in estimating the foraging intake of spiders."

Tso & Severinghaus (1998) argue that using dry weights will tend to underestimate the ingested biomass, and disproportionately so with increasing prey sizes. However, the ingested biomass they suggest measuring is still not a good estimate of the energy derived from the prey because a large proportion of this biomass will be the water responsible for the divergence of the plotted curves; water is not a source of metabolic energy. In very dry habitats, the water content of the biomass ingested from a prey item may indeed be of great importance, and the total volume of liquified food ingested will certainly be a factor in determining satiation level in situations where prey is not limiting. Wet biomass ingested will only be proportional to energy intake if the separate components of water and digestible biomass are in constant proportions (as assumed by Tso & Severinghaus) in different sized prey. This will only be the case if water content and digestible biomass both scale with size in exactly the same way. One might expect both to be approximately proportional to volume (i.e., $\propto \text{length}^3$) but the exact exponents would have to be determined empirically (see Schoener 1980), and their coefficients (0.7 for water and 0.1 for digestible macromolecules in the equation of Tso & Severinghaus) checked for constancy across prey size range.

An appropriate measure that is likely to be a direct function of energy intake from a prey item is total dry weight (= digestible dry weight + exoskeleton) less the weight of the dry exoskeleton rejected after feeding. The absolute intake of digestible dry weight must, of necessity, always be less than the total dry weight of the prey and will therefore fall below the lower curves in Tso & Severinghaus's fig. 1. Within this constraint, the shape of the digestible dry weight curve will depend on its allometric relationship with absolute size. Although digestible dry weight probably scales approximately $\propto \text{length}^3$ (but, again, see Schoener 1980) exoskeleton probably reflects more closely surface area (i.e., $\propto \text{length}^2$). As total dry weight increases with size, one would therefore expect a greater proportion to be represented by digestible material in larger prey items. Some evidence for this is provided by Rees (1986) who investigated the relationship between the fraction of total (wet) mass attributable to dry skeletal mass and total wet mass across taxa within six beetle families. The slopes of all six plots were negative (two-tailed sign test, $P = 0.03$), although only one was individually significant. Total mass was measured as wet rather than dry weight, but if the degree of tissue hydration is constant or, if variable, not a function of beetle size, these data suggest that skeletal mass decreases and, as a consequence, the remainder (digestible

mass) increases with total beetle mass (size). This is in direct contrast to the conclusions of Tso & Severinghaus quoted above—the use of total dry weight as a surrogate for energy availability will produce an underestimate that decreases with increasing prey size. If energy intake is the currency of interest when investigating spider foraging, ingested dry weight is the appropriate, and direct, measure to use.

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RESEARCH NOTE

A TEST OF POLLEN FEEDING BY A LINYPHIID SPIDER

Keywords: Araneae, nutrition, *Pinus*, cage

For several weeks starting in January or February each year, fallout of pine pollen forms a yellow coating on the upper surface of almost everything present in the xeric, upland habitats on the Lake Wales Ridge in south-central Florida. Juvenile orb-weavers, *Araneus diadematus* Clerck (Araneidae), and crab spiders, *Thomisus onustus* Walckenaer (Thomisidae), at high latitudes are known to greatly enhance their life expectancy in spring by feeding on pollen (Smith & Mommsen 1984; Vogeley & Greissl 1989). Hence, we reasoned that web spiders in Florida scrub might consume pine pollen adhering to their silk for added nutrition when insects typically are in short supply. We tested this idea using individually housed, female bowl and doily spiders, *Frontinella pyramitela* (Walckenaer) (Linyphiidae). We selected this spider because it is locally abundant on the Lake Wales Ridge in winter and its sheet webs become extensively coated with pine pollen.

We collected adult and subadult *F. pyramitela* ($n = 36$) at the Archbold Biological Station, Highlands County, Florida in February 1995 and transported them alive back to the laboratory in Missouri. We weighed the spiders to the nearest 0.01 mg and then placed them individually in cages made from recycled, 2-liter plastic carbonated beverage bottles. Each cage contained four vertical glass rods (20 cm \times 4 mm o.d.) arranged in a square \sim 5 cm on a side to provide support for a spider's web (Fig. 1). A cage was prepared by cutting off the bottom part of a transparent bottle, embedding the rods in a 2 cm thick layer of patching plaster poured into the bottom section, and taping the capped top section back on the bottom section after the plaster was dry. Once sealed in this manner, the in-

expensive bottle cage proved to be mold-free and almost airtight.

Two days after their introduction into the bottle cages at 22–26 °C under constant illumination, all spiders had spun typical sheet webs on the glass rods. On days 3, 8, and 13 we misted the contents of each cage with water sprayed through the bottle's orifice. On day 4 we assigned equal numbers of spiders ($n = 12$) at random to one of three treatments: Unfed, Pollen-Fed, and Fly-Fed. On days 4, 9, and 14 we uncapped the cage of each Pollen-Fed spider and manually stripped much pollen from two ripe strobili of the South Florida slash pine, *Pinus elliottii* Engelm. var. *densa* Little & Dorman, sufficient to coat the entire web. To retain nutrients, the strobili were kept frozen at –20 °C in plastic bags after collection at the Archbold Biological Station. On the same three days we fed 5–7 adult *Drosophila melanogaster* Meigen to each spider in the Fly-Fed group. On day 19, we opened every cage and re-weighed the spiders.

The initial masses of the spiders were highly uniform (Mean \pm S.E.M. = 2.26 ± 0.14 mg; Coefficient of Variation = 0.0080). But at the end of the tests, spiders given a diet of fruit flies had gained an average of 2.29 ± 0.61 mg. In contrast, the Pollen-Fed spiders each had lost 0.29 ± 0.07 mg, an amount statistically equivalent to the mass lost by an Unfed spider (0.24 ± 0.014 mg). The Fly-Fed spiders were significantly heavier than spiders in either of the other two groups (ANOVA, $F = 20.79$, $df = 2$, $P < 0.0001$). Hence, we conclude that *F. pyramitela* did not consume pine pollen in amounts sufficient to maintain body mass. In addition, extensive observations never revealed any behavior that might suggest this spider was actively consuming

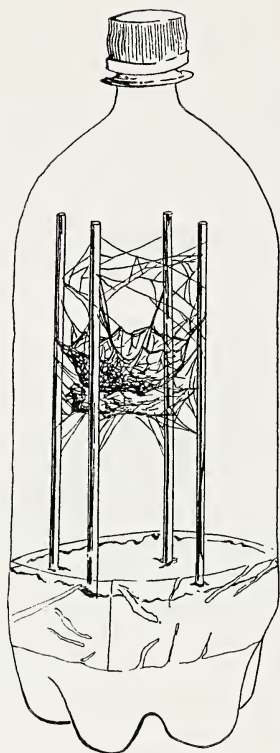


Figure 1.—Side view of the sheet web of *F. pyramitela* suspended from four glass rods inside a cage made from a transparent, 2-liter plastic, carbonated beverage “soda” bottle. The top of the bottle is held in place by wide adhesive tape. Removal of the tape allows one to have free access to the spider on its web.

pollen or removing pollen from its silk, although we often saw spiders attack fruit flies entrapped in their webs.

Pine pollen is an abundant, although short-lived resource that is known to be the preferred dietary component for the rare blister beetle, *Lytta polita* Say, which emerges in winter in south-central Florida (Carrel et al. 1990). This large insect consumes staminate *Pinus* cones, much as Americans eat corn-on-the-cob. Furthermore, chemical analysis showed that pine pollen is nearly as nutritious as pollen collected by honeybees foraging at nearby flowers (J.E. Carrel & J. Bull unpubl. data). Hence, even though bowl-and-doily spiders did not gain weight when offered pine pollen, it is likely that other species, in particular orb-weavers that ingest silk as they take

down their adhesive spirals, consume pine pollen trapped in their webs.

The soda bottle cages have proven to be very suitable for long term studies of linyphiid spiders. For example, we reared several generations of *F. pyramitela* in these cages, allowing us to rapidly repeat work on web building, predation, and the pheromonal basis of courtship in this spider (Suter & Renkes 1982, 1984; Suter & Hirscheimer 1986). In addition, we now are testing the chemical basis of prey discrimination by small araneids housed in the bottle cages. Because the cages are disposable, there is no possibility of carry-over of chemical residues from test to test.

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RESEARCH NOTE

COMPARISON OF THE FERTILITY BETWEEN *LOXOSCELES INTERMEDIA* AND *LOXOSCELES LAETA* SPIDERS (ARANEAE, SICARIIDAE)

Keywords: Fertility, sinanthropy, loxoscelism, egg-sac production

Envenomation by brown spiders of the genus *Loxosceles* Heineken & Lowe 1832 of North America, the Middle East, South Africa and South America commonly results in a local necrotic skin lesion and sometimes causes systemic effects that can lead to the death of the patient (Denny et al. 1964; Efrati 1969; Newlands 1982; Gerstch 1967; Gerstch & Ennik 1983; Futrell 1992). *Loxosceles* spp. are the most poisonous spiders in Brazil and children who develop the more severe systemic effects after envenomation nearly always die. At least three different *Loxosceles* species of medical importance are known in Brazil: *L. intermedia* Mello-Leitão 1934, *L. laeta* (Nicot 1849) and *L. gaucho* Gertsch 1967. More than 1500 cases of envenomation by *L. intermedia* alone are reported each year. Because of a lack of understanding of the mechanism of action of the venom, an effective treatment is not available.

Loxosceles are nocturnal and non-aggressive spiders. In the natural environment, they live under rocks, inside tree holes and other places that may serve as shelter. While some occupy hot and arid regions, others inhabit relatively damp areas. They also live in dark, dry places in houses, such as doorsteps, wall cracks, spaces behind pictures, furniture or even curtains, as well, in household rubbish and buildings (Gertsch 1967; Gertsch & Ennik 1983).

Loxosceles intermedia prevails in the urban environment of the states of Paraná and Santa Catarina (south region of Brazil) (Fischer 1994; Mattosinho et al. 1997). This species is restricted to the southern regions of South America including Brazilian Federal District (middle west region), the states of Rio de Ja-

neiro and São Paulo (southeast region), Rio Grande do Sul (south region), and also in Argentina. The distribution of *L. laeta* is much wider, and it can be found throughout South America including Peru, Chile, Ecuador, Brazil (from the state of Paraíba to the state of Rio Grande do Sul, from the northeast region to south region), Uruguay and Argentina. According to Gerstch (1967), *L. laeta* has also spread to some parts of North America, being found in Massachusetts and other locations due to its sinanthropy (Levi & Spielman 1964). In Brazil, *L. laeta* is also found in the same States as *L. intermedia*. It prevails in the south of Santa Catarina State (south region) (Mattosinho et al. 1997) and, in Curitiba city (Paraná State, south region) during June and July, although being less abundant than *L. intermedia*.

Although *L. intermedia* and *L. laeta* can be both found in the south region of Brazil, there has been a significant increase in the number of *Loxosceles* bites mainly associated with *L. intermedia* which seems to be positively correlated with the expansion of this species' range (Ribeiro et al. 1993). The present study was performed to compare the fertility of the two species reared in laboratory to better understand expansion of the *L. intermedia* population in the south region of Brazil.

This study was conducted in "Biotério de Criação e Manutenção de Aranhas" of the Immunochimistry Laboratory, Butantan Institute, São Paulo, Brazil. The spiders used in this study were collected in the town of Campo Alegre (Santa Catarina State, south region, Brazil) from June to August. The sampled group of females, fertilized in the natural environment, comprised 108 *L. intermedia* and

47 *L. laeta*. They were transferred to plastic boxes (9.5 cm diameter \times 5.5 cm high) and kept in the laboratory under normal environmental temperature and relative humidity ($19.3^\circ\text{C} \pm 2.8$ and $81.3\% \text{ RH} \pm 2.07$). The spiders were fed with cockroach nymphs (*Pycnoscellus surinamensis*, Dictyophthera, Blaberidae) or with darkling beetle larvae (*Tenebrio mollitor*, Coleoptera, Tenebrionidae) twice a month.

All specimens were observed weekly for eight months. During this period, the following variables were evaluated: number of egg sacs per spider, total number of eggs per egg sac, total number of spiderlings hatched per egg sac and time for spiderlings to hatch. The mean of the values was compared using a two-tailed *t*-test at a significance level of 0.05.

The results show that the differences between the mean number of egg sacs per spider of *L. intermedia* [1.79 ± 0.83] and *L. laeta* [1.67 ± 0.84] were not statistically significant (Fig. 1A). However, the mean number of eggs per egg sac per spider and as well as the total number of eggs was significantly higher for *L. laeta* (Fig. 1B). Mean times to hatching for *L. laeta* spiderlings were significantly greater for *L. laeta* than *L. intermedia* (Fig. 1C). The percentage of hatched spiderlings was high but did not reveal statistically significant differences between the two species.

The mean number of the egg sacs produced per female was similar for both species, the maximum was five egg sacs for *L. intermedia* and four for *L. laeta*; the minimum was one egg sac for both species. These results differ from those of Galiano & Hall (1973) who described up to 15 egg sacs per female of *L. laeta*. However, those females were mated under laboratory conditions, which makes it possible to record all the egg sacs produced per female. Nevertheless, it cannot be excluded that, because they were not feeding in the natural environment, they may possibly have had enhanced fertility. Hite et al. (1966) described up to five egg sacs per female of *L. reclusa*, while Fischer (1996) observed up to three egg sacs for *L. intermedia*. As in our study, these authors observed adult females collected in their natural environment, and therefore the possibility that they had produced previous egg sacs could not be excluded. The *Loxosceles* spiders can live from 3–7 years (Galiano & Hall 1973; Lowrie 1980, 1987). The age of



Figure 1.—Comparison of the fertility of *Loxosceles intermedia* and *Loxosceles laeta* collected as fertilized adults. (A) Number of egg sacs per spider, (B) Number of eggs per egg sac, and (C) Time to hatching of spiderlings. The results are expressed as mean \pm SD.

the spiders collected can also affect the quantity of egg sacs produced per spider.

The analysis showed that *L. laeta* exceeded *L. intermedia* in both the total number of eggs produced per female and per egg sac. These results may reflect differences in body weight between the two species. The females of *L. laeta* were larger and heavier [$1.161 \text{ cm} \pm 0.52$; $0.2115 \text{ g} \pm 0.026$] than *L. intermedia* [$1.096 \text{ cm} \pm 0.093$; $0.1260 \text{ g} \pm 0.035$] (Cristina de Oliveira et al. 1999; G. de Andrade

unpubl. data), and such differences might allow the former species to have a greater oviposition potential. It is well-known that fecundity tends to be correlated with body mass for female invertebrates, including spiders (Higgins 1992; Fischer 1996; Schneider 1996).

Under the conditions of this study, the means of the total number of eggs produced per spider and per egg sac were greater for *L. laeta* which suggests that a greater fertility could be ascribed to *L. laeta* than to *L. intermedia*. If so, these considerations suggest that the significant expansion of *L. intermedia* in the south region of Brazil is not due to a great reproductive rate of that species. Studies on the ecological aspects of the sinanthropy of both species, as well as the possible environmental alterations in the south region of Brazil, may explain the predominance of the *L. intermedia* spiders.

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RESEARCH NOTE

GROUP DISPERSAL IN JUVENILE *BRACHYPELMA VAGANS* (ARANEAE, THERAPHOSIDAE)

Keywords: Tarantula behavior, spiderling aggregation

Cutler & Guarisco (1995) summarized the literature accounts of juvenile dispersal by mygalomorph spiders and noted that such observations were rare. None of those reports involved the Theraphosidae because juvenile behaviors associated with dispersal had not been described for this family. This report documents three instances of aggregative juvenile dispersal by theraphosid spiders observed in the Lamanai Archaeological Reserve, Orange Walk District, Belize (17°45'08"N, 88°39'25"W).

On 26 May 1998, and 8–9 June 1999, juvenile *Brachypelma vagans* (Ausserer 1875) were observed in large aggregations and were apparently dispersing from their natal burrows in a manner not previously described for any spider. Only one other large theraphosid occurs in the area, *Crassircus lamanai* Reichling & West 1996, and juveniles of this species are distinguished by their uniform light gray color, as opposed to juvenile *B. vagans* which are pale with a black spot on the abdomen. In addition, *C. lamanai* prefers cleared habitat and is rare in dense forest where these observations were made. Each encounter took place at night between 2015–2115 h on a dirt road leading into old growth secondary forest. In each instance, groups of spiderlings (numbering 72, 76, and 135 respectively) were walking in single file, forming a line which slowly snaked its way along the road. From a distance the processions resembled a column of ants, and the largest of these aggregations formed a line 1.09 m in length (Fig. 1). The spiders maintained close proximity to one another while walking, often lightly touching the abdomen of the individual ahead of them with their front legs. The spiderlings were observed

for 8–12 m as they moved diagonally across the road and into the vegetation. A thorough daytime search of the surrounding area revealed that the nearest burrows occupied by adult *B. vagans* were ~50 m from the site where the June observations were made.

The spiders were disturbed by the direct beam of a flashlight; or if approached too closely, they stopped their progression and scattered slightly. Once the disturbance ceased they reassembled in single file and proceeded as before. On two occasions road dust was sprinkled across the spiderlings' path in a small gap which had formed in the line. When they reached the road dust the spiderlings stopped and began milling about as the ones ahead of them continued on their way. After a minute, the spiderlings began moving in the same general direction as before and appeared to recapture the trail beyond the dust.

The tarantula occupying the front of the line changed frequently. As the leading spider took a slight turn to the left or right, the spider behind it would move ahead and take over the lead while the previous leader would insert itself farther back in line. This replacement of the leading spider occurred every 7–10 cm.

Terrestrial theraphosid spiders often occur in dense, local aggregations, with burrows abundant in some locations but absent in adjacent sites which represent similar habitat (Baerg 1958). These assemblages exhibit underdispersed distribution patterns, with nearest neighboring burrows in closer proximity than would be predicted by chance alone (Reichling 1999). Some fossorial lycosids also occur in clusters. *Geolycosa xera archboldi* McCrone 1963, a sandhill endemic of central Florida, typically disperse less than one meter

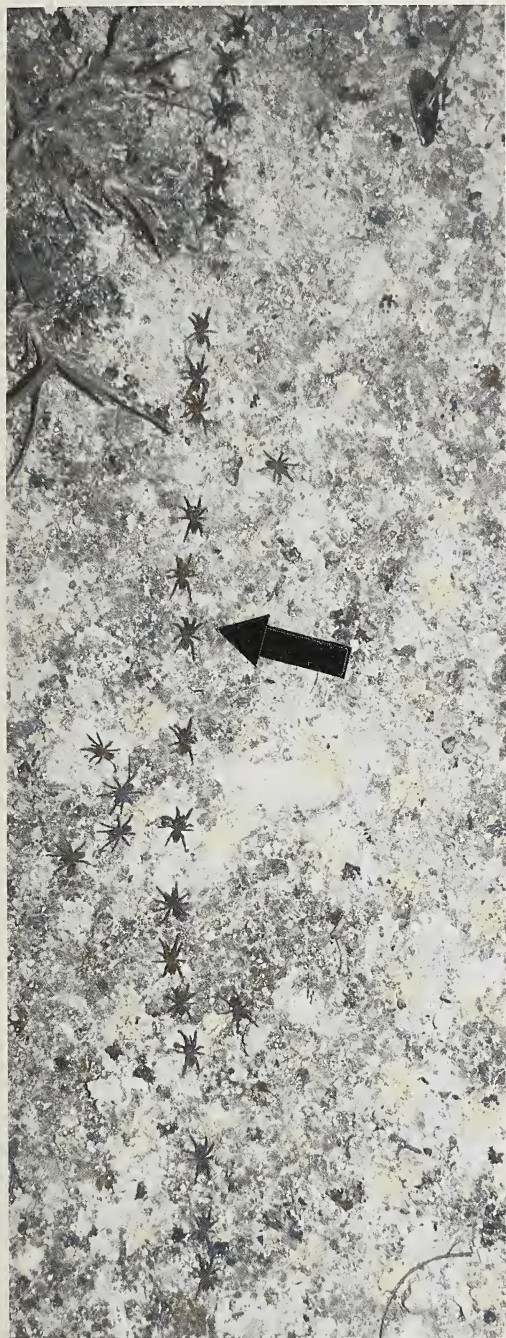


Figure 1.—Line of juvenile *Brachypelma vagans* (arrow) moving across a dirt road in the Lamanai Archaeological Reserve, Orange Walk District, Belize. Some spiderlings have scattered due to the beam of a flashlight.

from their maternal burrow and settle within one hour, leading Marshall (1995) to propose that the burrow aggregations characteristic of this taxon are due to highly restricted juvenile dispersal distances. This mechanism does not appear satisfactory for explaining theraphosid aggregations in light of the considerable distance from potential maternal burrows that dispersing *B. vagans* were seen.

The observations described here suggest a plausible explanation for the clustered spatial patterns of theraphosid spiders. With the exception of mature males, terrestrial theraphosids are rarely observed far from their burrow, and it is likely that an individual's burrow site remains close to the location where it was first established by the juvenile. If the mass movement of single clutches of *B. vagans* continues until the juveniles settle and establish residence, it would result in the aggregations characteristic of tarantulas in Belize and elsewhere. The hypothesis that these clusters are composed primarily of siblings can be tested.

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RESEARCH NOTE

HUNTING AND FEEDING BEHAVIOR OF ONE *HETEROPODA* SPECIES IN LOWLAND RAINFOREST ON BORNEO (ARANAE, SPARASSIDAE)

Keywords: *Heteropoda*, hunting behavior

Spiders in the genus *Heteropoda* Latreille 1804 (Sparassidae) are distributed in tropical Asia and Australia, with the exception of the cosmopolitan *Heteropoda venatoria* (Linnaeus 1758) (see Roewer 1954; Brignoli 1983; Platnick 1989, 1993, 1998; P. Jäger per. commun.). With the exception of the Australian species (Davis 1994), the genus *Heteropoda* as well as the entire family are unrevised (Jäger 1998). To date, two nominal species of *Heteropoda* have been described from Borneo, *H. hosei* Pocock 1897 and *H. obtusa* Thorell 1890; a generic revision is necessary to distinguish between these species (Jäger pers. commun.). *Heteropoda* sp. from lowland rainforest in Kinabalu Park (Sabah, Malaysia) were observed in the field and laboratory. Voucher specimens, including two females, one male, and two juveniles, are deposited at the Field Museum of Natural History.

Between April and July 1998, one of us (SA) conducted nightly surveys along streams in lowland rainforest (600 m elevation) near Poring Hot Springs in Kinabalu Park (Sabah, Malaysia, 6°03'N, 116°42'E). Surveys were conducted along 100 m transects at three sites in Kinabalu Park and one site in an agricultural area. Visual surveys were conducted by walking slowly along each edge of the stream, searching for spiders in, under, and on all substrates between the stream banks. We recorded the size of each spider and its position on the transect. We recorded the substrate type selected by each spider, the horizontal distance from the edge of the stream, the vertical distance from the ground, and the nearest aquatic microhabitat type.

We encountered a mean of 6.5 ± 3.1 spi-

ders per night on 100 m stream transects in primary forest. Significantly fewer spiders (2.2 ± 1.6) occurred along streams in an agricultural area nearby (independent samples $T = 3.85$, $df = 13.5$, $P = 0.002$). Spiders were unevenly distributed, with a mean distance between spiders of 16.8 ± 18.1 m in primary forest and 19.1 ± 23.3 m in the agricultural area. Spiders exhibited stereotyped microhabitat selection. Ninety-three percent of the spiders in primary forest ($n = 154$) and 75% of the spiders in the agricultural area ($n = 22$) perched, facing downward, on boulders and small rocks at the edge of streams. In both primary forests and the agricultural area, spiders perched less than a meter from the water and the ground. On average, spiders perched a distance of 0.93 ± 1.27 m from the water in primary forest, and 0.69 ± 0.80 m in the agricultural area. Spiders perched a mean distance of 0.44 ± 0.57 m from the surface of the water or the ground in both habitats. Spiders remained motionless unless disturbed. At one instance we observed a spider jumping from its perch on a rock and diving into the water. There it remained submerged for a period of time long enough for us to lose sight of it. We did not observe prey capture in the field.

Thirteen spiders were housed in the laboratory for up to four weeks, each in 15 gallon (57 liters), clear, plastic cages with screen lids. Every five days the spiders were fed three prey items in cafeteria trials. Prey items included three species of frog larvae, *Leptobranchium montanum* (Megophryidae), *Meristogenys orphnocnemis* (Ranidae), and *Rana signata* (Ranidae), one species of fish, *Glan-*

Table 1.—Prey selection by *Heteropoda* sp. in laboratory trials.

Prey	Species	<i>n</i> offered	<i>n</i> eaten
Cockroaches	unknown	20	15
Fish	<i>Glanyops hanitschii</i>	20	10
Large tadpoles	<i>Leptobrachium montanum</i>	30	3
Small tadpoles	<i>Rana signata</i>	10	0
	<i>Meristogenys orphnocnemis</i>	10	0

yops hanitschii, and an unidentified species of cockroach. During each trial all spiders were given the same three prey. Live prey were placed in shallow, plastic trays (10 × 15 × 1 cm) filled with water on the floor of each cage. Cockroaches were released on the floor of the cage. We observed behavior of the spiders for up to 1 hour following the initiation of a feeding trial. We recorded attack, capture and prey handling behaviors.

Between trials, spiders consistently oriented themselves above shallow trays of water in their cages. Spiders rested vertically on cage walls, facing downward, with their pedipalps and two front appendages resting lightly in the water. During cafeteria trials, spiders remained motionless until movement of the prey elicited a predatory response. Spiders generally attacked prey in the water by quickly lurching forward and piercing the skin of the prey with their fangs. After a successful capture, spiders climbed the cage wall to begin prey manipulation. Spiders used the front appendages and chelicerae to “fold” the prey in half, using silk to reinforce the fold. Spiders then fastened the prey to the cage wall with silk, released hold of the prey, and began a stereotyped weaving procedure. Spiders straddled the prey and moved in a counter-clockwise direction, rotating the body 360° directly above the prey while encircling the prey with silk. The spiders continued weaving until prey items were wrapped in tight packages of silk. After prey capture and manipulation, spiders began feeding on the prey. Spiders generally completed feeding less than 24 hours after prey capture and discarded the shrunken body of the prey at the bottom of the cage.

In cafeteria trials, spiders consumed 75% of the cockroaches, 50% of the fish, and 10% of the large tadpoles (*L. montanum*) offered. Spiders did not capture or consume small tadpoles (*M. orphnocnemis* and *R. signata*). In trials with small and large tadpoles, spiders

captured and consumed only large tadpoles. In trials with fish and large tadpoles, both prey were taken. In trials with cockroaches and tadpoles, or cockroaches and fish, spiders captured and consumed cockroaches.

Capture of cockroaches was significantly different from capture of aquatic vertebrate prey. Spiders were alerted by movement of the prey, and they attacked the prey with a swift and precise jump. One spider attacked a cockroach with a vertical jump of over 20 cm (pers. obs.). Spiders did not use silk to subdue invertebrate prey. No terrestrial attacks were observed in the field, although we observed one spider in the process of consuming a moth.

Hunting on the water surface has so far been reported from three spider families in various parts of the world (Pisauridae, Trechaleidae, and Lycosidae). Hunting on the water surface and feeding on aquatic and non-aquatic prey is known from three pisaurid genera; the worldwide *Dolomedes* Latreille 1804 (Bleckmann & Rovner 1984; Williams 1979), the African-Asian *Thalassius* Simon 1885 (Abraham 1923; Sierwald 1988), and the South American *Ancylometes* Bertkau 1880 (Schiapelli & Gerschman 1970); among the Trechaleidae it is known for members of the South American genus *Trechalea* Thorell 1869 (Berkum 1982). Among the Lycosidae, members of the genus *Pirata* Sundevall 1832 live in marshes and move over the water surface (Bristowe 1923; Ehlers 1939). Diving behavior is reported for *Dolomedes* species and *T. spinosissimus* (Sierwald 1988). This represents the first report of members of the family Sparassidae hunting on the water surface.

We are grateful to the Malaysian government for permission to work in Sabah. We thank the director of Sabah Parks, Datuk Lamri Ali and the deputy director, Francis Liew, for permission to work in Kinabalu Park and for temporary staff housing at the field site.

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BOOK REVIEW

Lycosids in China. C.M. Yin, X.J. Peng, L.P. Xie, Y.H. Bao & J.F. Wang. 317 pp. Hunan Normal University Press, Changsha 1997. ISBN 7-81031-599-4/Q.017.

The arachnological research activities in China have increased considerably during the last decades, promoted by and associated with increasing awareness of the role of spiders in agricultural issues (Song 1996). The literature on Chinese spiders has grown substantially mainly due to the studies performed by various research groups in the country. One of them is active at the Hunan Normal University in Changsha under the leadership of Prof. Changmin Yin, and a number of comprehensive books on spiders have originated from this group [*Spiders in China, One Hundred New and Newly Recorded Species of the Families Araneidae and Agelenidae* including papers by C.M. Yin et al. and J.F. Wang et al. (1990), *Salticids in China* by X.J. Peng, L.P. Xie, X.Q. Xiao & C.M. Yin (1993), *Fauna Sinica: Arachnida Araneae: Araneidae* by C.M. Yin, J.F. Wang, M.S. Zhu, L.P. Xie, X.J. Peng & Y.H. Bao (1997)].

A recent contribution from this group is *Lycosids in China*. As stated in the foreword, the book does not encompass all wolf spider species currently known to occur in China but is based on the material available in the collection of the Department of Biology at Hunan Normal University. Most material therefore comes from more southern parts of this vast country. Regrettably, for 'outsiders', the book is addressed mainly to Chinese reading arachnologists. No English summary is given, but there are bilingual (Chinese/English) figure legends.

Descriptions of 135 species distributed among 13 'traditional' genera are given, including lists of synonyms, comments on affinities with other species, habitat (for some of the species) and distribution, particularly within China. It is to be noted that the genus

Ocyale Audouin 1826 is now represented in China by the recently (1997) described *O. qiongzongensis* Yin & Peng which is included in the book. Keys to subfamilies, genera and species are supplied. [The subfamily Hippasinae is maintained, encompassing a mixture of genera (*Ocyale*, *Pirata* Sundevall 1833, *Venonia* Thorell 1894, *Hippasa* Simon 1885) currently allocated to other subfamilies, in despite of Hippasinae presently being placed as a junior synonym of Lycosinae (cf. Dondale 1986; Zyuzin 1993)]. Illustrations are provided for all species, at least of the habitus (not very informative) and the copulatory organs. For some species the copulatory organ of only one sex is shown despite both sexes are known (the other sex not present in the collection). For a number of species additional illustrations are given, showing, e.g., the inflated bulb. Details of the macerated female receptacular complex are given for several species; information which hardly has been given as a routine in comparable monographic treatments. For many species more details of the male palp are still wanting, i.e., the configuration of the terminal part of the bulb and the detailed shape of the embolus.

The number of species within each genus as treated in the book is: *Evippa* Simon 1882 (2), *Xerolycosa* Dahl 1908 (1), *Hippasa* (4), *Ocyale* (1), *Pirata* (12), *Venonia* (1), *Alopecosia* Simon 1885 (13), *Arctosa* C.L. Koch 1847 (17), *Hogna* Simon 1885 (2), *Lycosa* Latreille 1804 (16), *Trochosa* C.L. Koch 1847 (8), *Pardosa* C.L. Koch 1847 (56), *Wadicosa* Zyuzin 1985 (2).

Several species are described as "sp. nov." though the names were already introduced in original descriptions (in Roman letters) by various author groups elsewhere (in issues of

either *Acta Arachnologica Sinica* or *Korean Arachnology* from 1997, antedating the publication date, 1 December 1997, of the present book). Only four of the species treated seem to have been originally described in this book, viz. "*Alopecosa disca* Tang et al., sp. nov.," "*Alopecosa wenxianensis* Tang et al.," "*Arcotosa liujiapingensis* sp. nov.," and "*Pardosa alboannulata* sp. nov." (names cited as they appear in the book).

From the illustrations it is apparent that there are a number of misidentifications. The following serve as examples only and is not meant to be a complete listing (for which the reviewers have insufficient knowledge): The figures referring to certain species, e.g., *Xerolycosa nemoralis* (Westring 1861), were apparently drawn from material belonging to other species. The epigynum in ventral view attributed to *Pardosa schenkeli* Lessert 1904 reminds one more of *P. hanrasanensis* Jo & Paik 1984 (from Korea); the latter on the other hand is listed as a synonym of what is stated to be *Pardosa bifasciata* (C.L. Koch 1834). *Pardosa anchoroides* Yu & Song 1988 was recently synonymized with *P. adustella* Roewer 1951 (by Logunov & Marusik 1995). The illustrations meant to show the *Pardosa atrata* (Thorell 1873) male were clearly drawn from another species, and the drawings attributed to the *Pardosa lapponica* (Thorell 1872) female were made from another, possibly undescribed, species. The illustrations ascribed to *Pardosa uncifera* Schenkel 1963 do not match the type material examined by us. Without details of the terminal apophysis of the bulbus, it is impossible to judge whether the authors really had *Pardosa monticola* (Clerck 1757) at hand. The illustrations of *Pardosa multivaga* Simon 1880 make us suspect that this species may not even belong in *Pardosa*.

There are scattered misspellings, e.g., "*krotochvilli*" instead of *kratochvili* throughout (in *Alopecosa*), "*dividi*" instead of *davidi* (syno-

nym of *Alopecosa licenti*), etc., author of *Pardosa astrigera* is L. Koch, not his father C.L. Koch. Several of the references given in the foreword and the introductory chapter do not appear in the list of literature cited at the end.

Despite the linguistic problems and the limited coverage of lycosid species from northern China—the title is accordingly "*Lycosids in China*" not "The Lycosids of China"—this book is a valuable tool for researchers outside China interested in taxonomic problems of East Asian wolf spiders. It will, above all, serve as a useful iconotheca and a source for taxonomic inspiration for those of us who do not master Chinese.

Both reviewers are grateful to Prof. Yin for copies of the book and to Mrs. Fang Fang, ichthyologist at the Swedish Museum of Natural History, for translation of certain passages in the book.

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The AAS Fund for Arachnological Research (AAS Fund) is funded and administered by the American Arachnological Society. The purpose of the fund is to provide research support for work relating to any aspect of the behavior, ecology, physiology, evolution, and systematics of any of the arachnid groups. Awards may be used for field work, museum research (including travel), expendable supplies, identification of specimens, and/or preparation of figures and drawings for publication. Monies from the fund are not designed to augment or replace salary.

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Lombardi, S.J. & D.L. Kaplan. 1990. The amino acid composition of major ampullate gland silk (drag-line) of *Nephila clavipes* (Araneae, Tetragnathidae). *Journal of Arachnology* 18:297–306.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1–4.—*A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us* holotype male; 33, 34. *A-us y-us* male. Scale = 1.0 mm.

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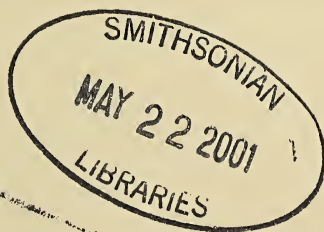
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THE JOURNAL OF ARACHNOLOGY

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Cover photo: Ballooning pisaurid (Araneae, Pisauridae) from Upper Souris National Wildlife Refuge, North Dakota. (Photo by Bryan Reynolds)

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A NEW SPECIES OF THE GENUS *KIMULA* (OPILIONES, MINUIDAE) FROM THE DOMINICAN REPUBLIC

Abel Pérez González and Luis F. de Armas: Departamento de Invertebrados, Instituto de Ecología y Sistemática, A.P. 8029, C.P. 10800, Habana 8, Cuba

ABSTRACT. *Kimula cokendolpheri* new species is described from the Central Range of the Dominican Republic, West Indies. It is the first non-fossil species of this genus recorded from Hispaniola.

Keywords: Opilionids, *Kimula*, West Indies, Dominican Republic

The Antillean genus *Kimula* Goodnight & Goodnight 1942 includes species that are found on the islands of Puerto Rico (*K. elongata* Goodnight & Goodnight 1942), Cuba (*K. tuberculata* Goodnight & Goodnight 1943, *K. levii* Šihavý 1969, *K. banksi* Šihavý 1969, *K. goodnightorum* Šihavý 1969, *K. turquensis* Šihavý 1969; and *K. botosaneanui* Avram 1973) (Cokendolpher & Camilo-Rivera 1989). On St. Johns, U.S. Virgin Islands, it is represented by an undescribed species, and in the Dominican Republic a female of *Kimula*? was found in amber that has a confirmed date of 25–40 MYA (Cokendolpher & Poinar 1992).

Kimula cokendolpheri new species is the first known living species of the genus *Kimula* from Hispaniola. However, if speciation of this group in Hispaniola is similar to that on Cuba (where there are other undescribed species, pers. obs.), it is likely that additional new species of *Kimula* will be found in Hispaniola.

METHODS

We studied material from the collections of the invertebrates of Hispaniola that is deposited in the Instituto de Ecología y Sistemática (IES) of the Ministerio de Ciencia, Tecnología y Medio Ambiente, Havana, Cuba. The nomenclature of the dorsum follows the usage of Maury (1991). We denote the body divisions as: prosoma, mesotergum (areas I, II, III, and IV), lateral margin, and posterior margin (denoted as area V by other authors). Dorsal scute is the sum of the mesotergum and its posterior margin. Measurements are given in mm and were made with a dissecting microscope equipped with an ocular micrometer.

Kimula cokendolpheri new species (Figs. 1–9)

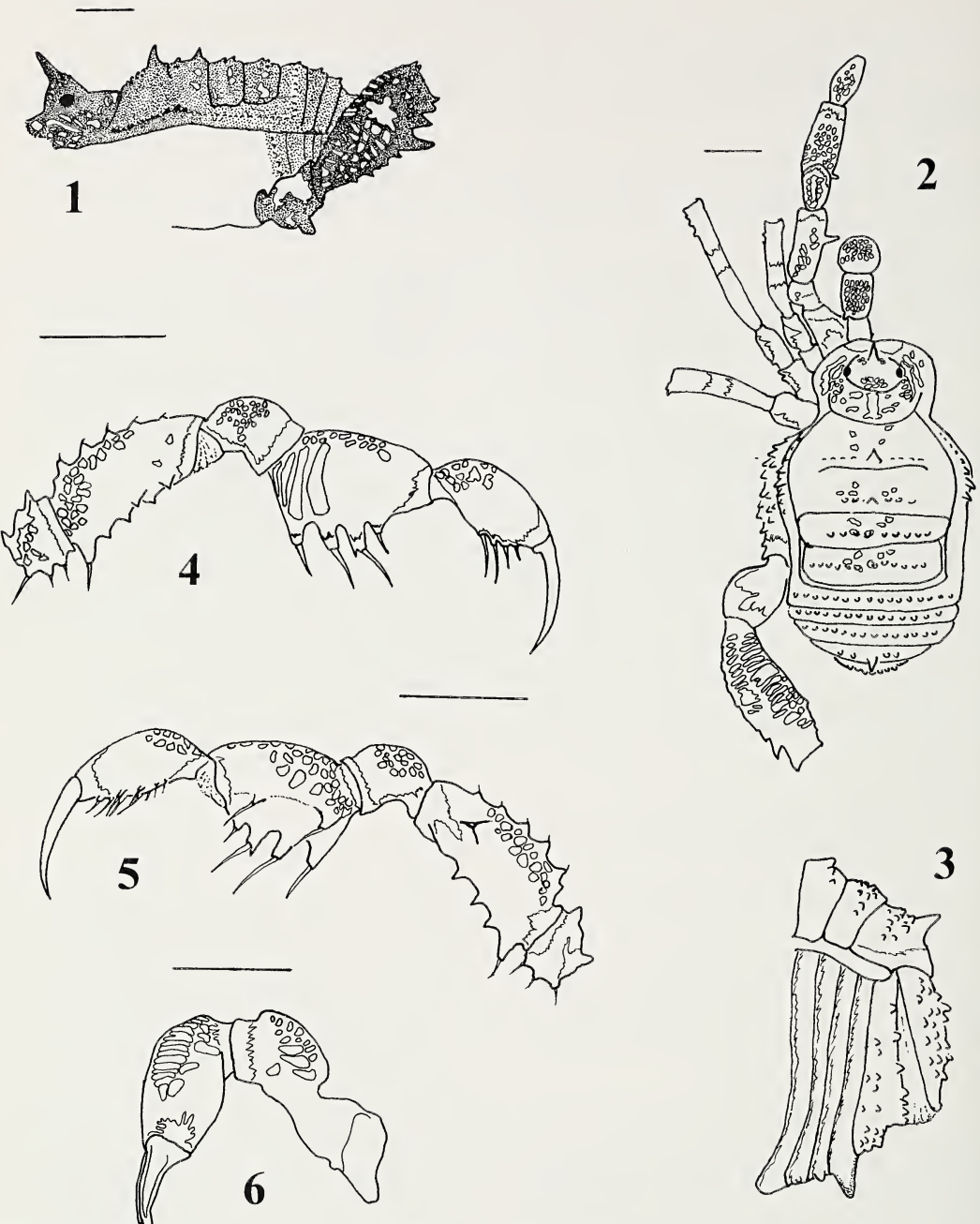
Type specimens.—Male holotype and two male and four female paratypes collected in Casabito, Constanza, provincia La Vega, Dominican Republic beneath stones on 27 September 1987 by A. Abud and L.F. de Armas. Deposited in the IES.

Distribution.—Known only from the type locality.

Etymology.—The specific epithet is a patronym in honor of James C. Cokendolpher, who has studied the opilionid fauna of the Antilles.

Diagnosis.—Total length 5.00 with area I lacking a median line and armed with a stout median spine similar to that of area II. Femurs of the pedipalps armed dorsally with a series of tubercles terminating in setae. Trochanter IV armed with a blunt ventroproximal tubercle. Tarsal formula: 4, 9-13, 5, 6. Distinctive male genitalia as shown in Figs. 7–9. *Kimula cokendolpheri* new species has two characters that are recorded for the first time in this genus: the median spine of areas I and II and the presence of tubercles on the dorsal surface of the femoral palp. These characters permit clear separation of this species from others in this genus.

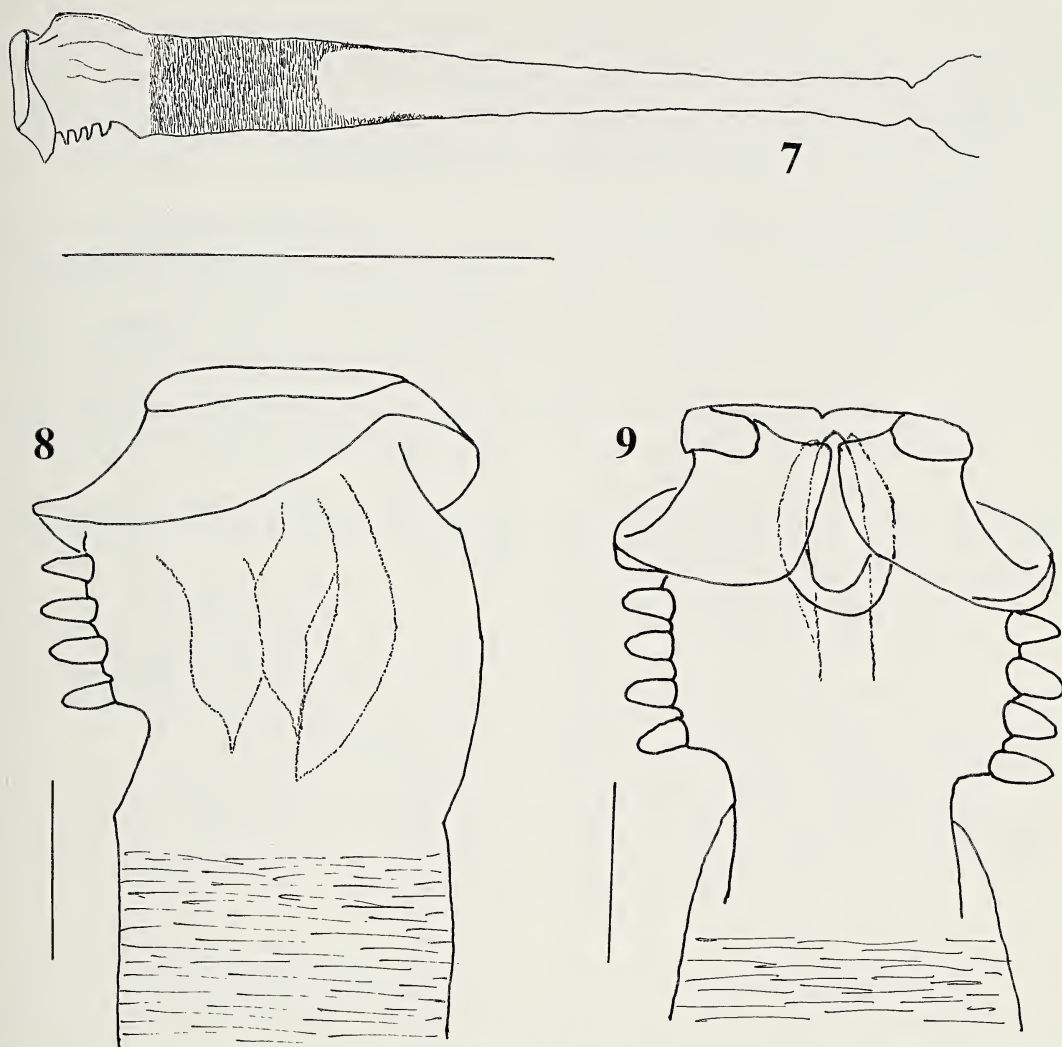
Description.—*Male:* Body brown. The chelicerae, pedipalps, legs, and prosoma bear yellowish patches and in some aspects appear reticulated. Trochanters of legs I, II, and III with dorsal yellowish markings. Ocular tubercle prominent, granular, armored with an erect, anteriorly inclined spine between the eyes (Fig. 1). Areas of the mesotergum distinct, covered irregularly by granules and tu-



Figures 1–6.—External morphology of *Kimula cokendolpheri* new species. 1. Lateral view; 2. Dorsal view; 3. Lateral view of opisthosoma; 4. Retrolateral view of right pedipalp; 5. Prolateral view of right pedipalp; 6. Medial view of right chelicera. Scale bars = 1 mm.

bercles, terminated in a small apical setae, inner areas with similar projections in the form of large spines: the first situated on the central portion of the posterior margin of area I and the second, smaller, occupying the same po-

sition in area II. Area I without a transverse median line. Areas I and II separated by an incomplete furrow. Dorsal scute with sinuous lateral margins and a straight posterior margin; these margins present a longitudinal row



Figures 7-9.—Penis of *Kimula cokendolpheri* new species. 7. Ventrolateral view (scale = 1 mm); 8. Lateral view of extreme distal region (scale = 0.1 mm); 9. Dorsal view of extreme distal region (scale = 0.1 mm).

of tubercles that are more evident and denticulate at the level of furrow II; this region achieves its maximum width at the level of furrow II. Tergites free with a longitudinal row of tubercles terminating in setae. Free tergite III has a median spine (Fig. 2); anal operculum with numerous short tubercles (Fig. 3). Retrolateral surface of coxa III with a distal tubercle, coxa IV very well developed and strongly tuberculated on its prolateral surface. Ventrally, all coxae granulated. Sternites free with a longitudinal row of granules; free sternite IV with a median spiny apophysis; free sternite V with two rows of longitudinal tu-

bercles one at the anterior margin and another on the posterior, separated by a furrow (Fig. 3). Pedipalp (Figs. 4, 5): the coxa has a ventral tubercle with apical setae, dorsally there are two proximal tubercles, one external and one internal; trochanter with five tubercles that possess apical setae, one dorsal and four ventral; femur with five or six small dorsal tubercles that bear fine apical setae, ectolaterally with a tuberculate proximal spine and with four or five tubercles and, on the anterior half of the internal surface, with tuberculate spines having large bases; patella unarmed; tibia ventrally with four tuberculate spines on its ex-

ternal border and two tuberculate spines on its internal border; tarsus with four ventral tuberculate spines on its external border and three ventral tuberculate spines on its internal border. Chelicerae (Fig. 6): basal article with a strong distal elevation on whose outer posterior border there is a small tubercle; distal articles with small tubercles terminated in setae. Legs lack tarsal processes and scopulae; legs I and II with all their articles, except the tarsae (which are unarmed), covered by tubercles that reach their greatest development in the ventral region of the femur. Leg IV is the most well-developed and is strongly armored with tubercles and spines, except for the tarsus, the trochanter has a characteristic blunt ventral tubercle (Fig. 1) and the femur is notably enlarged with a ventral row of strong spines. The patella and the tibia are strongly tuberculate and at their apices have very enlarged and globose ventral tubercles. Tarsal formula: 4(2), 9–13(2), 5(3), 6(3). Male genitalia as shown in Figs. 7–9. Measurements of the male holotype: total length = 5.6; prosoma + scutum = 4.7; maximum width 3.4; leg I = 7.7 (trochanter 0.5, femur 1.7, patella 0.8, tibia 1.3, metatarsus 2.0, tarsus 1.4); leg II = 11.3 (trochanter 0.7, femur 2.4, patella 1.1, tibia 1.8, metatarsus 2.5, tarsus 2.8); leg III = 8.3 (trochanter 0.6, femur 1.7, patella 0.8, tibia 1.4, metatarsus 2.3, tarsus 1.5); leg IV = 12.6 (trochanter 1.0, femur 2.8, patella 1.7, tibia 2.5, metatarsus 2.9, tarsus 1.7).

Female: Similar to the male in appearance, but smaller. The spines are reduced and femur IV differs markedly and is not as enlarged. Trochanter IV has a ventrodistal spine rather than the blunt tubercle characteristic of the male. The free sternite lacks the spiny median apophysis. Measurements of the one female paratype: total length = 4.9; prosoma + scutum = 3.9; maximum width 2.8; leg I = 7.7 (trochanter 0.6, femur 1.5, patella 0.8, tibia 1.2, metatarsus 1.9, tarsus 1.7); leg II = 10.7 (trochanter 0.8, femur 2.2, patella 1.1, tibia 1.6, metatarsus 2.3, tarsus 2.7); leg III = 7.8 (trochanter 0.7, femur 1.5, patella 0.8, tibia 1.3, metatarsus 2.0, tarsus 1.5); leg IV = 11.2 (trochanter 1.1, femur 2.4, patella 1.2, tibia 2.1, metatarsus 2.8, tarsus 1.6).

Natural history.—The specimens studied were collected at an elevation of approximately 1000 m above sea level, beneath stones and in forest litter in a very humid forest at the margins of a stream that abounded in tree ferns.

ACKNOWLEDGMENTS

We are grateful to J.C. Cokendolpher for sending literature and, particularly, to the late Emilio E. Maury, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia," for the training provided to the first author and for the valuable literature he provided. Norman Platnick kindly lent the holotype of *Kimula elongata*. I especially want to thank Brent D. Opell for the translation to English and for his help in the publication of the present article.

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SYSTEMATICS OF THE GENUS *DYSDERA* (ARANEAE, DYSDERIDAE) IN THE EASTERN CANARY ISLANDS

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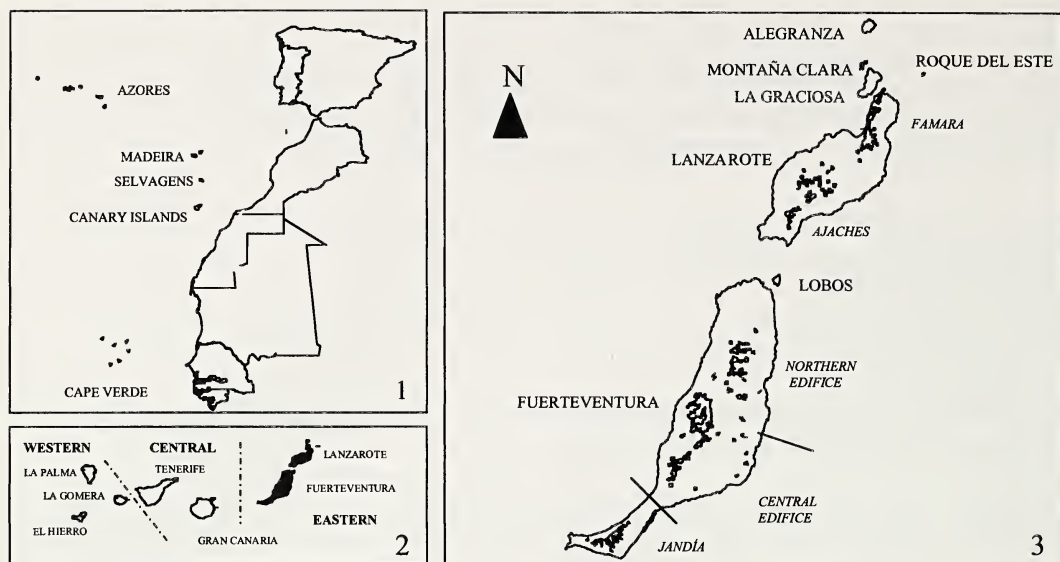
ABSTRACT. The circum-Mediterranean spider genus *Dysdera* has undergone an outstanding species radiation in the volcanic archipelago of the Canary Islands. The present study deals with the endemic species that inhabit the older and ecologically distinct islands of Fuerteventura, Lanzarote and their nearby islets. A new species, *Dysdera sanborondon*, is described. The male of *D. spinidorsum* Wunderlich 1991, is described for the first time. Five species are redescribed: *D. alegranzaensis* Wunderlich 1991; *D. lancerotensis* Simon 1907; *D. longa* Wunderlich 1991; *D. nesiotis* Simon 1907, and *D. spinidorsum* Wunderlich 1991. The species *D. liostethus* Simon 1907 is proposed to be a senior synonym of *D. clavisetae* Wunderlich 1991 and its presence in the eastern islands is considered to be doubtful. A neotype is designated for *D. nesiotis*. The distribution of *D. alegranzaensis* is extended to Lanzarote and the other northern islets. *Dysdera nesiotis* is reported for the first time in the eastern Canaries. Morphological affinities and distribution patterns are discussed. The remarkably lower number of endemic species harbored by the eastern islands, when compared with other Canarian islands similar in size but younger in age, is proposed to be the result of a major extinction event in the eastern Canaries due to climatic change.

Keywords: Spider taxonomy, oceanic islands, colonization, extinction

Studies in oceanic archipelagos have become crucial in the rise and development of evolutionary thinking and the present Darwinian paradigm. To date, the role played by the different islands has been highly biased in favor of the Pacific Archipelagos (the Hawaiian Islands and the Galapagos). Nevertheless, in the last few years a growing number of studies on the systematics of such diverse groups as lizards (Thorpe et al. 1994, 1995; González et al. 1996; Rando et al. 1997), beetles (Juan et al. 1995, 1996a, 1996b, 1998) or plants (Böhle et al. 1996; Francisco-Ortega et al. 1996; Kim et al. 1996; Mes & T'Hart 1996) have revealed an additional excellent model for the study of biodiversity in the Atlantic region: the Macaronesian archipelagos, and in particular the Canary Islands.

The genus *Dysdera* Latreille 1804 comprises more than 200 species of nocturnal wandering spiders spread over the circum-Mediterranean region. About a quarter of these species have been described from the Macaronesian archipelagos (Fig. 1), representing the most species-rich spider genus reported in them. Nevertheless, the Macaronesian endemics are far from being equally distributed. The Canary Islands harbor 43 of these endemics, while five endemics have been documented from Madeira (Denis 1962; Wunderlich 1994). The Açores, Cabo Verde and Selvagens Islands each have a single species (Arnedo unpubl. data; Berland 1936; Kulczynski 1899). The unusually large number of species in the Canaries suggests many evolutionary and ecological questions. A research program is currently underway to resolve some of the problems posed by the genus in the archipelago (Ribera & Arnedo 1994; Arnedo & Ribera

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Figures 1–3.—1, Location of the Canaries and the remaining Macaronesian archipelagos; 2, The Canary Islands; 3, Fuerteventura, Lanzarote and the islets.

1996; Arnedo et al. 1996; Arnedo & Ribera 1997).

Although the geological processes that created the Canary Islands are still a matter of debate (Anguita & Hernán 1975; Carracedo et al. 1998a 1998b), the first island most likely arose about 25 My ago. The seven main islands lie 100 km from the northwestern coast of Africa in a roughly straight line (Fig. 2). A geographical gradation in their geological age exists, the islands being older in the east and becoming younger to the west. The estimated geological age for each island is: Fuerteventura 20–22 My, Lanzarote 15–19 My, Gran Canaria 14–16 My, Tenerife 11.6–14 My, La Gomera 10–12 My, La Palma 1.6–2 My and El Hierro 0.8–1 My (Cantagrel et al. 1984; Mitchell-Thomé 1985; Ancochea et al. 1990; Coello et al. 1992; Fuster et al. 1993; Ancochea et al. 1994, 1996). Unlike some well-known oceanic archipelagos such as the Hawaiian Islands, the growth of the islands extended over long periods of time (Coello et al. 1992), and volcanic activity is cyclic and is not restricted to the younger islands. These features together with the absence of a subduction region which would promote subsidence of the older islands, as is the case in several Pacific archipelagos (Paulay 1994), allow the islands to reach later stages of ecological succession. The eastern Canaries are

the emergent regions of a volcanic ridge, running parallel to the African coast in a NNE–SSW direction (Coello et al 1992). It comprises two main islands, Fuerteventura at the SSW and Lanzarote at the NNE end, and several islets: Lobos, between the two big islands, and La Graciosa, Roque del Este, Roque del Oeste, Montaña Clara and Alegranza, to the north of Lanzarote (Fig. 3). The maximum ocean depth between these islands is barely 40 m and thus it is very likely that they were connected during glaciation periods. The islands are the result of five volcanic complexes that arose from the ocean in a temporal succession: the peninsula of Jandía 20.7 Mya, the Central edifice 22.5 Mya, the northern edifice 17.0 Mya in Fuerteventura (Ancochea et al. 1996) and Ajaches 15.5 Mya and Famara 10.2 Mya in Lanzarote (Coello et al. 1992). The eastern Canaries have undergone several sub-aerial cycles of volcanic activity. A major gap in activity between the Miocene and the Pliocene periods brought about an extensive erosion of the edifices. Postmiocene activity was limited to central and northern Fuerteventura and Lanzarote (Coello et al. 1992). In these regions, recent volcanic activity, and historical eruptions in the case of Lanzarote, have been documented. Apart from the lack of recent volcanic activity, the peninsula of Jandía, in southern Fuerteventura, is characterized by its

“ecological” isolation. It is separated from the rest of the island by an isthmus which is extensively covered with eolic sands.

The geological structure of the sea floor between the eastern Canaries and Africa is obscured by thick sediments. Surprisingly, subfossil ostrich eggs have been found in the islands. These data have driven some authors to claim a continental origin for the eastern Canaries with subsequent episodes of volcanic activity (Sauer & Rothe 1972). However, geological data accumulated during the last few years strongly disagree with this view, pointing to a strictly oceanic origin of the islands.

Before the present study five *Dysdera* species were reported to be present in the eastern Canaries (Wunderlich 1991; Arnedo et al. 1996): *Dysdera longa* Wunderlich 1991, and *D. spinidorsum* Wunderlich 1991 from Fuerteventura; *D. liostethus* Simon 1907 from Lanzarote; *D. alegranzaensis* from the islet of Alegranza and *D. lancerotensis* Simon 1907, reported from the two major islands. Two of these species, *D. liostethus* and *D. spinidorsum*, were known from single specimens: a male and a female respectively.

After taking into account their age and size, the number of *Dysdera* endemic species harbored by the eastern Canaries is remarkably low when compared with the remaining islands in the archipelago. The three endemic species from Fuerteventura represent less than half the number of endemic species known from the similarly sized but younger Gran Canaria, and much less than the 21 endemic species from the slightly larger but younger Tenerife. Lanzarote has the same number of endemic species as La Palma, which is similar in size but ten-fold younger, while eight species are known from La Gomera, only half its size and age. It is possible that the depauperate species composition in the eastern islands is the result of undersampling or, more generally, of the poor taxonomic knowledge of these islands. However, if these disparities are in fact real, the ecological and evolutionary processes that underlay them need to be elucidated.

METHODS

Material was made available from scientific institutions (as well as personal collections) and collection expeditions to the islands by the authors. The following colleagues and mu-

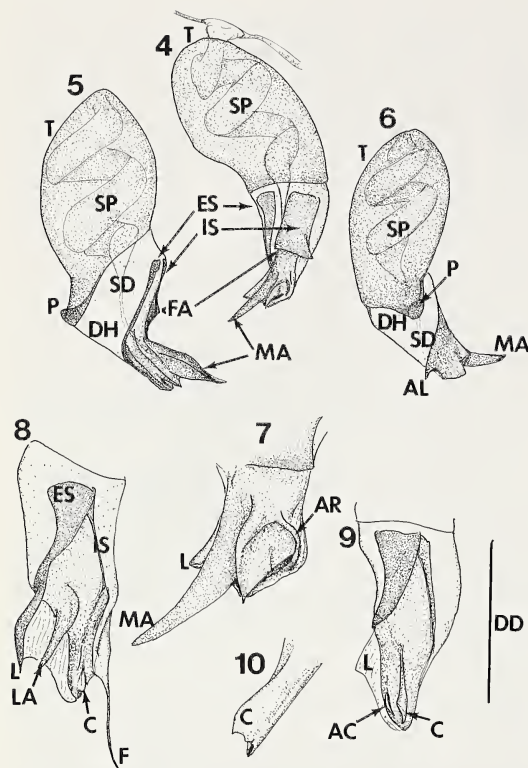
seums kindly supplied material for the present study: Dr. E. Enghoff from the Zoologisk Museum of Copenhagen (ZMK), O. Escolà from the Museu de Zoologia de Barcelona (MZB), Dr. P.D. Hillyard from the Natural History Museum of London (BMNH), Dr. P. Oromí from the Universidad de La Laguna (UL), Dr. G. Ortega from the Museo de Ciencias Naturales de Santa Cruz de Tenerife (MCNT), Dr. C. Rolland from the Muséum National d'Histoire Naturelle de Paris (MNHN) and Miguel Villana (MNCN). Material from the authors' expeditions is stored in the collection of Arachnids of the University of Barcelona, Spain (UB).

Character definition and terminology.—

Characters were examined under a Wild Heerbrugg (12–100× magnification) dissecting microscope and measurements were taken using an ocular micrometer. Female vulvae were removed and muscle tissues were digested using a KOH (35%) solution before observation. Male bulbi and spinnerets were removed, cleaned by means of ultrasound and examined using a HITACHI S-2300 Scanning Electron Microscopy at 10–15 Kv. Drawings of dorsal carapace, ventral chelicera, male palp and female endogyne were made with the aid of a drawing grid.

Characters examined for taxonomic revision and their diagnostic resolution have been discussed elsewhere (Arnedo et al. 1996; Arnedo & Ribera 1997). Leg spination was recorded using the codification method fully described in Arnedo & Ribera (1997). Structures of the male bulbus and female endogyne were mostly named following Deeleman-Reinhold & Deeleman (1988). However, after examination of a large number of continental representatives it was realized that some of the terms included very different and probably non-homologous characters. With the aim of clarifying character terminology a full description and definition of characters are provided for *Dysdera* male and female genitalia (see also Arnedo & Ribera 1997).

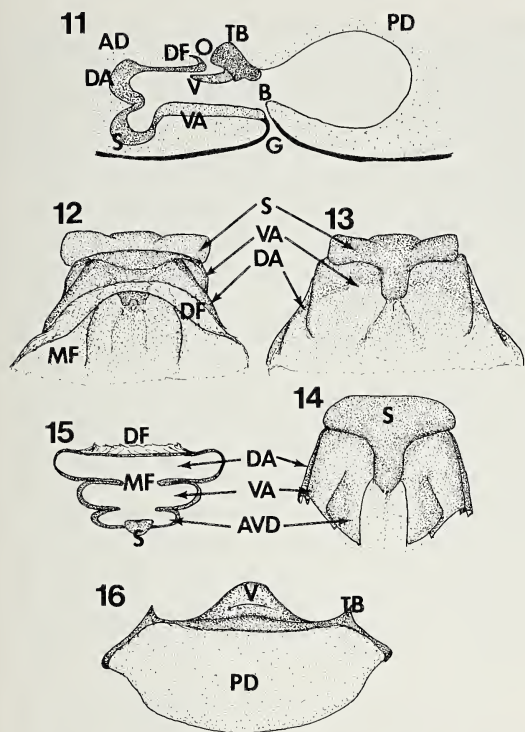
Male bulbus: (Figs. 4–10) The genus *Dysdera* has one of the most complex bulbs in the whole family Dysderidae. Schult (1980, 1983) was the first to establish the homologies between the *Dysdera* bulb and the spider ground plan as suggested by Kraus (1978). In *Dysdera*, the basal and medial haematodochae as well as the sclerites I (= subtegulum) are very



Figures 4–10.—Diagrams showing the male copulatory bulbus characters discussed in text. 4, Frontal view; 5, External view; 6, Posterior view. 7–10, Different types of DD: 7–9, Frontal view; 10, DD type 9, Distal tip internal view.

reduced and hardly visible. On the other hand, the sclerite II or tegulum (T) is very well-developed, representing in most cases half of the bulbus, and holds a posterior apophysis (P). The T externally covers the spermophore (= reservoir or sperm duct) (SP). The distal division (DD) of the bulb includes the membranous distal haematodocha (DH), which includes the seminiferous duct (SD) inside, and the sclerite III (= embolic division). The DH is usually truncated at its distal tip, where the seminiferous duct opening is found. Sometimes, the internal distal tip of the DH projects as a finger-like structure. Sclerite III or embolic division, which is located on the anterior side of the bulb, is divided into two branches, the internal branch or internal sclerite (IS) and the external one (ES). Schult (1980, 1983) proposed that the posterior apophysis (P) and the external sclerite (ES) were homologues to the median apophysis and the conductor, respectively, of the Araneoclada. However, both

the median apophysis and the conductor are developed from the claw fundamental dorsal lobe, which separates early in its ontogeny from the rest of the bulb. As a consequence, the two structures should be intimately related and more or less independent from the rest of the sclerites (Coddington 1990). Nevertheless, the posterior apophysis and external sclerite of *Dysdera* are not only clearly separated one from the other but they form part of the sclerites, the tegulum and the embolic division, respectively, that are supposed to be independently derived during ontogeny. Therefore, the posterior apophysis and the external sclerite are better considered as apomorphic features of *Dysdera*. The relative development and degree of fusion of the external and internal sclerites is variable. The IS is usually more or less straight. A frontal apophysis (FA) is sometimes present in IS proximal region. In some species, an expansion of the distal internal part of the DH has been observed. When this happens the IS usually covers the external and anterior sides of the expansion, thus assuming the appearance of a crest, here referred to as the “DD internal expansion.” However, this structure is different from some crest-like ridges that may be present on the anterior distal part of the IS. These ridges may be straight and parallel to the IS, which characterizes the Canarian *Dysdera* species, or arch-like and opened to the distal tip. Hereafter, the former crest is referred to as C while the second one is simply called “arch-like ridge” (AR). The distal external margin of the IS may be already expanded. This expansion is sheet-like and laterally projected over the ES and is called the “lateral fold” (LF, not shown). The lateral fold has several levels of development. In some Canarian species, it is very reduced and only visible at the distal tip of the DD, being called the “additional crest” (AC). In other instances, the LF is strongly sclerotized and apophysis-like, and is referred to as the “medial apophysis” (MA). The ES is markedly bent in the middle, going from the anterior side to the posterior one. Therefore, the distal part of the DH is anteriorly covered by the IS and posteriorly covered by the ES. The ES is usually laterally expanded in a sheet-like structure called the “lateral sheet” (L). The external margin of this structure may be sclerotized. The degree of development of the L is very variable. In some



Figures 11–16.—Diagrams showing the vulva characters discussed in text. 11, Sagittal section of the female genital region; 12, Anterior diverticle, dorsal view; 13, Anterior diverticle (AVD absent), ventral view; 14, Anterior diverticle (AVD present), ventral view; 15, Transversal section of the anterior diverticle (AVD present), posterior view; 16, Posterior diverticle, dorsal view.

Canarian species, a small apophysis, anteriorly projected, has been recorded, and is named the “lateral sheet apophysis” (LA). Posteriorly, the ES border may be fused to the DH or may form a rim, which is called the “additional lateral sheet” (AL). The border of this rim is generally smooth, although some species have a toothed margin. Finally, in some species the distal tip of the AL is projected in a flagellum (F).

Vulva: (Figs. 11–16) The female genitalia are entirely internal. Mcheidze (1972) coined the term “endogynum” to refer to this structure in contrast to the “epigynum” or external female genital structures of the entelegyne spiders, although the more general term vulva was preferred in this study. The genitalic furrow (G), located in the anterior ventral region, gives rise to the internal bursa (B) which is divided into two diverticles, an anterior div-

erticle (AD) and a posterior one (PD). These two pouches are also separated dorsally by the oviduct opening (O). The posterior diverticle is usually more developed than the anterior one and is mostly membranous with the single exception of the transversal bar (TB). This structure is located on the anterior dorsal margin of the posterior diverticle. There is a semi-circular sheet-like expansion on its anterior border, the “bursal valve” (V), which fits with the anterior diverticle, closing the oviduct opening to the bursa. The anterior diverticle holds nearly all the female genitalic characters used in the taxonomy not only of the genus but of the entire family. The anterior diverticle is further divided into two pouches, a dorsal diverticle and a ventral one, by a middle invagination of its lateral walls. This fold is called the “major fold” (MF). The dorsal anterior diverticle is commonly highly sclerotized, and is referred to as the “dorsal arch” (DA). The dorsal side of the DA, called the “dorsal fold” (DF), is responsible for locking the V. Additional lateral folds may be found in the DA. The ventral diverticle is called the “ventral arch” (VA) in contrast to the DA. It roughly corresponds to the “ventral plate” defined by Deeleman-Reinhold & Deeleman (1988). The anterior part of the VA is bent upwards, limiting the most anterior margin of the DA. An additional lateral fold of the VA, resulting in an “additional ventral diverticle” (AVD), has been reported in some Canarian *Dysdera*. The level of sclerotization of the VA is very variable and is very useful in both taxonomy and phylogeny. Unfortunately, drawings of the ventral vulva are very scarce in the taxonomic studies of the Dysderidae. Finally, a T-shaped, completely sclerotized spermatheca (S) is found in the anterior ventral region of the VA.

Spinnerets and associated spigot glands were assigned after Platnick et al. (1991). All taxonomic characters were recorded in DEL-TA format (Dallwitz 1980, 1993). All measurements are in mm. Abbreviations used in text and figures are as follows. Eyes: AME: anterior medial eyes, PME: posterior medial eyes, PLE: posterior lateral eyes; cheliceral teeth: B: basal tooth, M: medial tooth, D: distal tooth; male copulatory bulb: T: tegulum, SP: spermophore, DD: distal division, IS: internal sclerite, FA: frontal apophysis, ES: external sclerite, DH: distal haematodoca, SD:

seminiferous duct, C: crest, AR: arch-like ridge, MA: medial apophysis, AC: additional crest, LF: lateral fold over L, between internal and external sclerites, L: lateral sheet, LA: lateral sheet apophysis, AL: additional lateral sheet at back internal border, F: flagellum, P: posterior apophysis; female genitalia: G: genitalic furrow, B: internal bursa, AD: anterior diverticle, PD: posterior diverticle, O: oviduct opening, DA: dorsal arch, DF: dorsal fold, MF: major fold, S: spermatheca, TB: transversal bar, V: bursal valve, VA: ventral arch, AVD: additional ventral diverticle; spinnerets: ALS: anterior lateral spinnerets, PMS: posterior medial spinnerets, PLS: posterior lateral spinnerets, ms: major ampulate gland spigot, ps: polar pyriform gland spigot.

In order to test if the eastern islands were significantly poorer in number of endemic species than the remaining Canaries, the log-transformed number of *Dysdera* species in each island was plotted against the log-transformed island age. The regression coefficient and a 95% confidence interval were calculated for the whole set of islands and with the eastern islands removed.

RESULTS

Family Dysderidae

Genus *Dysdera* Latreille 1804

Dysdera alegranzaensis Wunderlich 1991

Figs. 17–22, 23–26, 27, 28

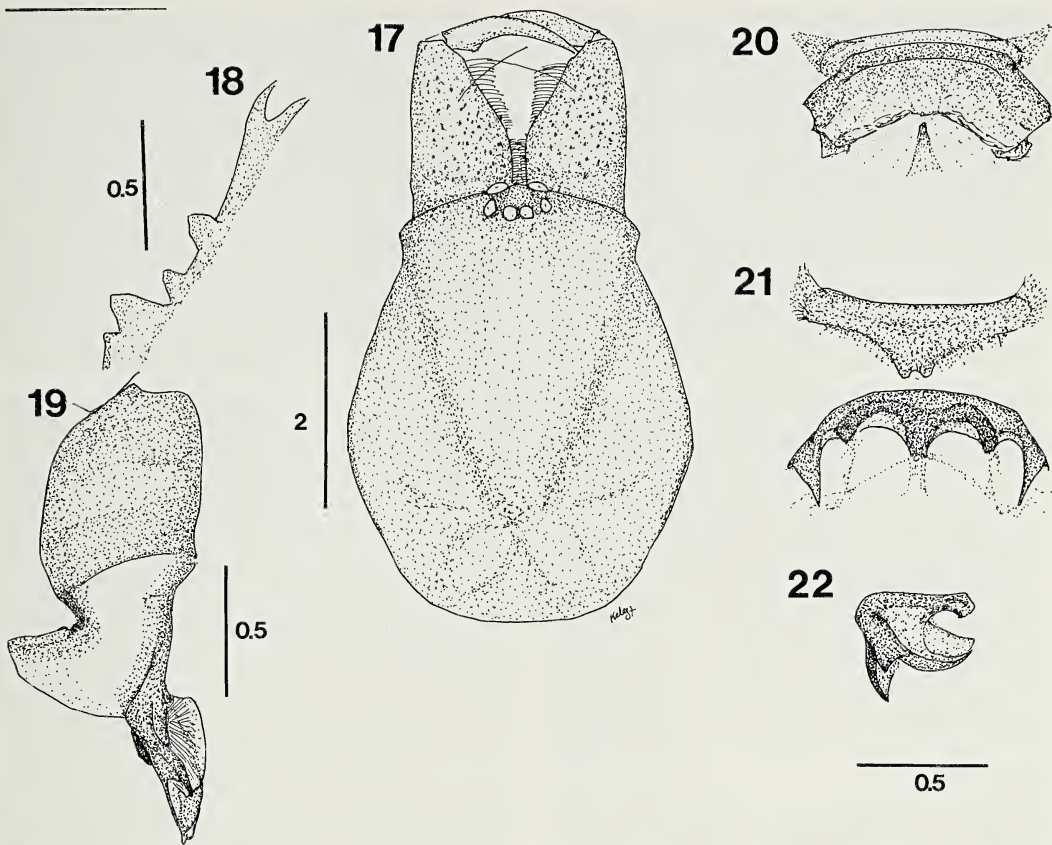
Dysdera alegranzaensis Wunderlich 1991: 287–288, figs. 7–9 [♂, ♀]. (Holotype male; from the ridge of the Caldera, Alegranza; June 1990; P. Oromí leg.; #02748, stored at UL; examined).

Diagnosis.—This species closely resembles *D. longa*, *D. nesiotis* and *D. spinisorsum* in somatic morphology and genitalia. Males are distinguished from the former species by showing a remarkable reduction in size of the bulb crest (C) (Fig. 24) and lacking the flagellum (Fig. 23). In females, vulva DA is distinctly shortened in length and back lateral margins are truncated (Fig. 20). Additionally, males can be distinguished from the sympatric *D. nesiotis* by having a distal division (DD) not bent in relation to the tegulum (T) (Fig. 19) and having the lateral sheet apophysis (LA) expanded over the lateral sheet (L) (Fig. 23).

Description.—*Male holotype:* (Figs. 17–

19, 23–24). Carapace (Fig. 17) 4.48 long; maximum width 3.43; minimum width 2.31. Brownish-red, frontally darker, becoming lighter towards back; slightly foveate at borders, slightly wrinkled with small black grains mainly at front. Frontal border roughly triangular, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders convergent (very slightly); rounded at maximum dorsal width point, back lateral borders straight; back margin wide, straight. AME diameter 0.25; PLE 0.2; PME 0.16; AME on edge of frontal border, separated from one another by about $\frac{2}{3}$ diameter, close to PLE; PME very close to each other, about $\frac{1}{3}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum orange, frontally darker, becoming lighter towards back; very slightly wrinkled, mainly between legs and frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 18) 1.96 long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-sized, 1.4; basal segment dorsal, ventral side completely covered with piligerous granulations. Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base; B > D > M (similar in size); D round, located roughly at center of groove; B close to basal lamina; M at middle of B and D. Front legs dark orange, back legs yellow. Lengths of male described above: fe1 3.73; pa1 2.56; ti1 3.77; me1 3.45; ta1 0.7; total 14.21; fe2 3.4; pa2 2.33; ti2 3.62; me2 3.54; ta2 0.79; total 13.68; fe3 2.61; pa3 1.44; ti3 1.72; me3 2.47; ta3 0.63; total 8.87; fe4 3.54; pa4 2; ti4 2.65; me4 3.4; ta4 0.79; total 12.38; relative length: 1-2-4-3; fe palp 2.23; pa palp 1.12; ti palp 0.93; ta palp 0.88; total 5.16. Spination: palp, leg1, leg2 spineless. Fe3d spines in one row: 2-3; ti3d spines arranged in two bands: proximal 1.2.1; distal 1.0.1; ti3v spines arranged in two bands: proximal 1.0.1; distal 1.0.0; with two terminal spines. Fe4d spines in two rows: anterior 3; posterior 6; ti4d spines arranged in two bands: proximal 1.1.1; distal 1.0.1; ti4v spines arranged in two bands: proximal 1.0.1; distal 1.0.1; with two terminal spines. Dorsal, ventral side of pedipalp covered with small piligerous grains (scarcely); very long hairs on back legs as well as on pedipalps. Claws with 8 teeth or less; hardly larger than claw width. Abdomen 10.7 long;



Figures 17–22.—*Dysdera alegranzaensis*. 17, Carapace, dorsal; 18, Left chelicera, ventral; 19, Right male bulb, external. 20–22, Vulva anterior diverticle: 20, Dorsal; 21, Ventral (S separated); 22, Lateral. Scale bars in mm.

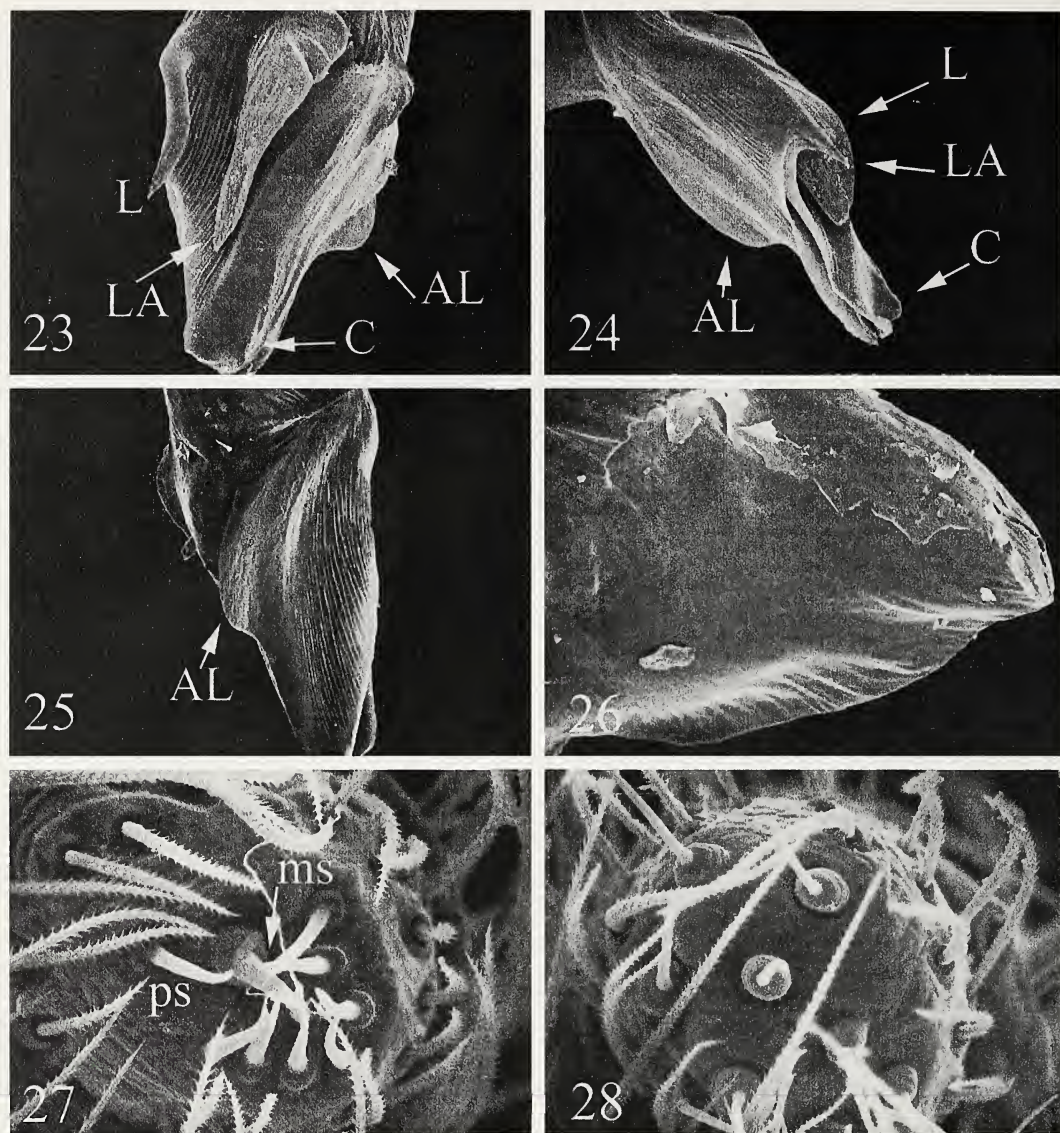
cream-colored; cylindrical. Abdominal dorsal hairs 0.144 long; thick, roughly straight, compressed, lanceolate; uniformly, thickly distributed.

Male copulatory bulb (Fig. 19) T as long as DD; external, internal distal border sloped backwards. DD not bent in lateral view; internal distal border markedly expanded. ES wider, more sclerotized than IS; IS continuous to tip. DD tip (Figs. 23–25) straight in lateral view. C present, short; distal end on DD internal tip; poorly developed; located close to DD distal tip; proximal border sharply decreasing; distal border truncated, upper tip not projected, rounded, external side smooth. LF absent. L well-developed; external border sclerotized, laterally markedly folded, distally projected; distal border divergent, continuous. LA present, sheet-like; as long as L, distally not fused. F absent. AL present, well-developed; proximal border in posterior view

smooth, not fused with distal haematodoca. P (Fig. 26) fused to T; perpendicular to T in lateral view; lateral length from $\frac{1}{2}$ – $\frac{2}{3}$ of T width; ridge present, perpendicular to T; distinctly expanded, right-angled; upper margin smooth; not distally projected; back margin not folded.

Female: (Figs. 20–22, 27, 28). All characters as in male except: Carapace 5.25 long; maximum width 4.02; minimum width 2.83. Deep red. Back lateral borders straight. AME diameter 0.25; PLE 0.21; PME 0.2.

Chelicerae 2.33 long; fang 1.57. $D = B > M$ (similar). Legs dark orange. Lengths of female described above: fe1 4.19; pa1 2.89; ti1 4.47; me1 3.73; ta1 0.74; total 16.02; fe2 3.63; pa2 2.61; ti2 3.45; me2 3.62; ta2 0.7; total 14.01; fe3 2.98; pa3 1.81; ti3 2.09; me3 2.98; ta3 0.74; total 10.6; fe4 3.96; pa4 2.28; ti4 2.89; me4 3.86; ta4 0.84; total 13.83; relative length 1-2-4-3; fe palp 2.14; pa palp 1.21; ti palp 0.98; ta palp 1.16; total 5.49. Spination:



Figures 23–28.—*Dysdera alegranzaensis*, right male bulbus. 23, DD frontal; 24, DD external; 25, DD posterior; 26, P internal. 27–28, *Dysdera alegranzaensis*, spinnerets. 27, Right ALS; 28, Right PLS.

palp, leg1, leg2 spineless. Fe3d spines in one row: 1; ti3d spines arranged in two bands: proximal 1.2.1; distal 1.0.1; ti3v spines arranged in two bands: proximal 1.0.0; distal 1.0.0; with two terminal spines. Fe4d spines in two rows: anterior 1; posterior 5; ti4d spines arranged in two bands: proximal 1.1.1; distal 1.0.1; ti4v spines arranged in two bands: proximal 1.0.1; distal 0.0.1; with two terminal spines.

Abdomen 10.74 long. Abdominal dorsal hairs 0.18. Vulva (Fig. 20–22) DA not distin-

guishable from VA; rectangular; DA twice as wide as long; DF wide in dorsal view. MF well-developed, completely sclerotized. VA frontal region completely sclerotized; posterior region sclerotized at most anterior area; tooth-shaped expansion from internal back border, not joined to lateral sclerotization, about half of DF lateral margins; AVD absent. S attachment projected under VA; arms as long as DA, straight; tips dorsally projected; neck as wide as arms. TB usual shape. ALS (Fig. 27) with PS; remaining piriform spigots

Table 1.—Intraspecific spination variability of *Dysdera alegranzaensis*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.2–4.1	0	0	1.0–1.1
Tibia 4 dorsal	0–1.0–1.1	0	0	0–1.0–1.0–1
Tibia 3 ventral	1.0.0–1	0.0.0–1	0	0–1.0.0–1
Tibia 4 ventral	1.0.1	0.0.0–1.	0	0–1.0.1
	Number of rows			Number of spines
Femur 3 dorsal		0–1		0–1
Femur 4 dorsal		2		1–3/2–6

more external than MS, arranged in two rows; 8 + 1 piriform gland spigots; PMS, PLS (Fig. 28) with 10–15 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 3.99–4.48, female from 3.57–5.25. AME separation from $\frac{3}{5}$ – $\frac{4}{5}$. PLE-PME from $\frac{1}{3}$ PME diameter to $\frac{1}{2}$. Carapace ornamentation somewhat reduced, nearly smooth. Chelicera relative size up to $\frac{2}{5}$ of the carapace length. Distal reduction of the chelicera granulations in some female specimens. Relative size of B and D variable, M always the smallest. Some female palps with ventral granulation. Spination variability in Table 1.

Additional material examined.—**Alegranza:** El Faro, 6 April 1993, 1♂, (P. Oromí, 2530 UL). Inside the Caldera, June 1990, 1juv., (P. Oromí, 2735 UL). Unknown locality, 3rd week March 1995, 1♂, (P. Oromí, 4106 UB); June 1990, 1♀, 3 juv., (P. Oromí, 2733 UL). **La Graciosa:** Caldera de Pedro Barba, 30 March 1996, 1♂, (P. Oromí, 3134 UB). Montaña del Mojón, 30 March 1996, 1♀, (P. Oromí, 3137 UB). **Lanzarote:** *Haría:* Montañas de Famara, around Mirador del Río, November 1988, 1♀, (A. Enghoff, 2670 ZMK); 22 February 1995, 3♂ (Arnedo, Ribera & Oromí, #2858–59, 4076 UB); 3♀, (Arnedo, Ribera & Oromí, #4080, 4104–5 UB). *Yaiza:* Montañas de Femés, Atalaya de Femés; 22 February 1995, 2♀, (Arnedo, Ribera & Oromí, #4089–90 UB).

Distribution.—Endemic species from Lanzarote and Northern islets.

Comments.—This species had only been reported from the rocky island of Alegranza before the present study.

Dysdera lancerotensis Simon 1907
Figs. 29–34, 36, 38–40, 41, 42

Dysdera crocata lancerotensis Simon 1907: 258.
(Types; 3♂3♀; unknown locality, Lanzarote; Ch.

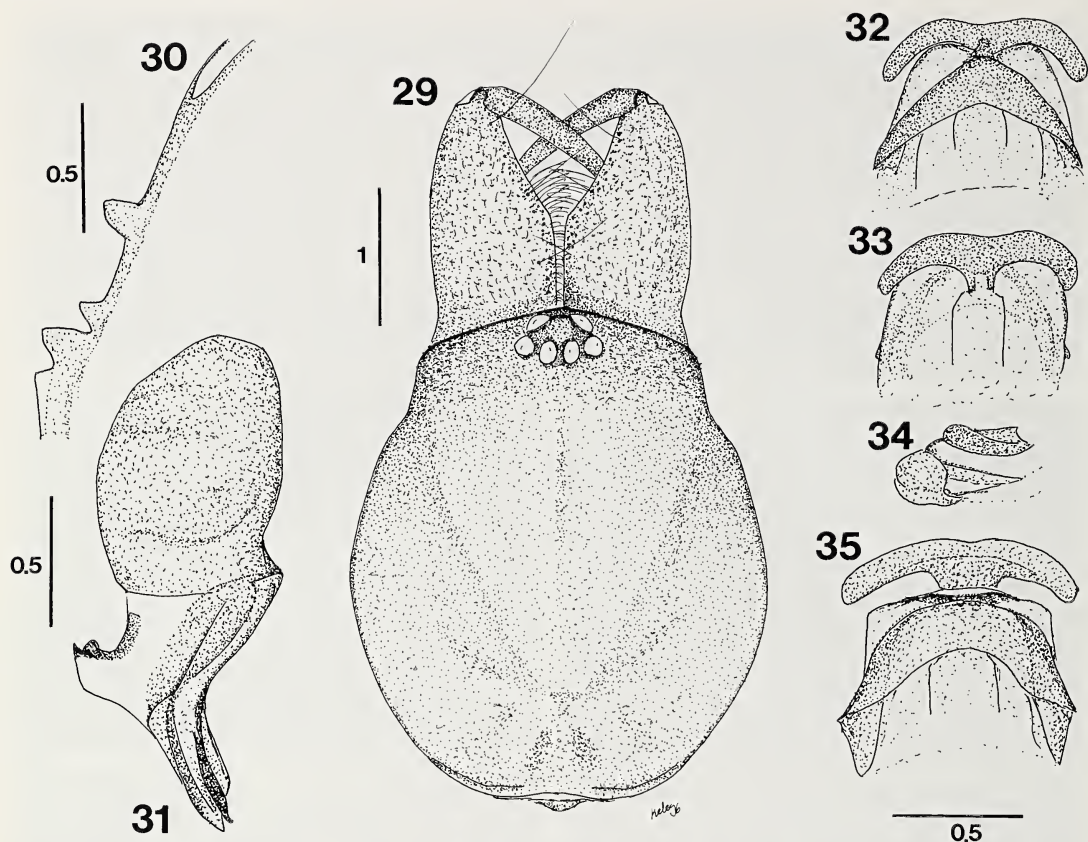
Alluaud leg.; #15586, stored at MHNP; examined).

Dysdera crocata lancerotensis: Denis 1941: 108.—Schmidt 1973: 360–361.

Dysdera lancerotensis: Wunderlich 1991: 296–298, figs. 50–52 [♂♀].

Diagnosis.—This species strongly differs from any other Canarian endemics. It closely resembles the cosmopolitan species *D. crocata* C.L. Koch 1839, from which both sexes can be distinguished by a spiny fel (although is not always so), males by the shape of the distal division (DD) tip in frontal view (Fig. 36–38) and the presence of two or three ridges on the posterior apophysis (P) upper margin (Fig. 39), and females by the dorsal shape of the dorsal arch (DA), the frontal projection of the ventral arch (VA) under the dorsal one (DA) and the presence of a tiny strip connecting frontally the dorsal arch with the spermatheca (S) attachment (Figs. 32, 35).

Description.—*Male:* (Figs. 29–31, 36, 38–39). Carapace (Fig. 29) 3.43 long; maximum width 2.87; minimum width 2.1. Uniformly dark red, slightly foveate at borders, slightly wrinkled with small black grains mainly at front. Frontal border roughly round, about $\frac{3}{5}$ carapace length; anterior lateral borders convergent (slightly); rounded at maximum dorsal width point, back lateral borders rounded; back margin wide, bilobulated; slightly stepped in lateral view. AME diameter 0.2; PLE 0.18; PME 0.14; AME slightly back from frontal border, separated from one another by about $\frac{2}{3}$ diameter, close to PLE; PME very close to each other, less than $\frac{1}{4}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; as long as wide at base; semicircular groove at tip. Sternum uniformly orange; very slightly wrinkled, mainly be-

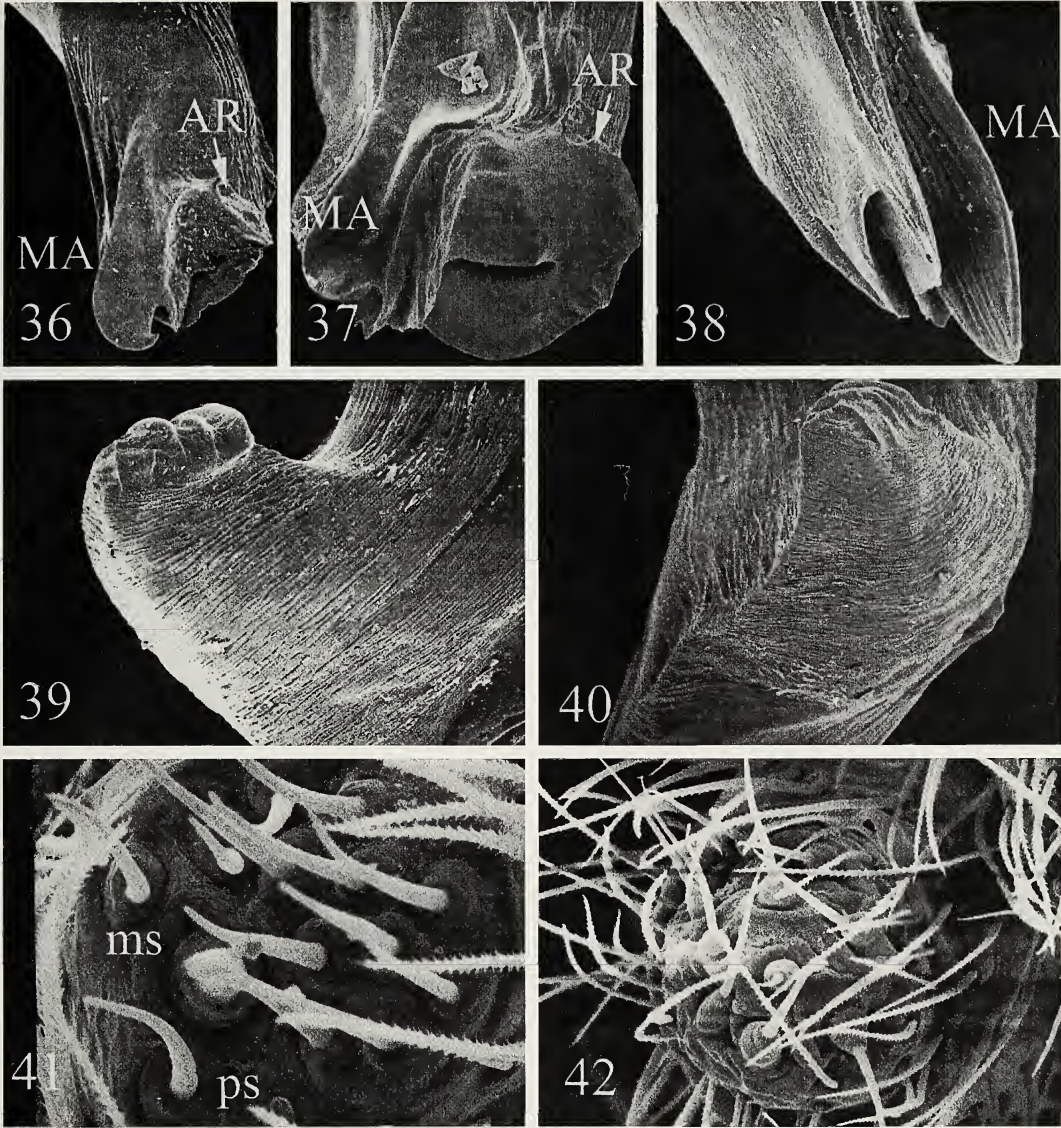


Figures 29–35.—*Dysdera lancerotensis*. 29, Carapace, dorsal; 30, Left chelicera, ventral; 31, Right male bulbus, external. 32–34, Vulva anterior diverticle: 32, Dorsal; 33, Ventral; 34, Lateral. 35, *Dysdera crocota*, vulva anterior diverticle, dorsal. Scale bars in mm.

tween legs and frontal border; uniformly covered in slender black hairs. Chelicerae (Fig. 30) 1.82 long, about $\frac{1}{2}$ of carapace length in dorsal view; fang long, 1.54; basal segment dorsal side completely covered with piligerous granulations (sparse), ventral side smooth. Chelicera inner groove long, about $\frac{1}{2}$ cheliceral length; armed with three teeth and lamina at base; $D=B>M$; D trapezoid, located roughly at centre of groove; B close to basal lamina; M close to B. Legs orange. Lengths of male described above: fe1 2.56; pa1 1.58; ti1 2.24; me1 2.33; ta1 0.65; total 9.36; fe2 2.28; pa2 1.4; ti2 1.96; me2 2.1; ta2 0.65; total 8.39; fe3 2; pa3 1.16; ti3 1.3; me3 1.77; ta3 0.56; total 6.79; fe4 2.47; pa4 1.3; ti4 1.91; me4 2.33; ta4 0.65; total 8.66; relative length: 1-4-2-3; fe palp 1.67; pa palp 0.93; ti palp 0.79; ta palp 0.93; total 4.32. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.0.1; distal 1.0.1; ti3v

spines arranged in one band: proximal 0.1.0; with two terminal spines. Fe4d spines in one row: 3; ti4d spines arranged in two bands: proximal 1.0.1; distal 1.0.1; ti4v spines arranged in one band: proximal 0.0-1.0; with two terminal spines. Dorsal side of frontal legs covered with small piligerous grains; ventral side covered with hairs, lacking grains. Claws with 8 teeth or less; hardly larger than claw width. Abdomen 4.48 long; whitish; cylindrical. Abdominal dorsal hairs 0.036 long; thin, roughly straight, not compressed, blunt, tip enlarged; uniformly, scantily distributed.

Male copulatory bulbus (Fig. 31) T as long as DD; external distal border straight; internal projected at middle. DD bent about 45° in lateral view; internal distal border not expanded. ES wider, more sclerotized than IS; IS continuous to tip. DD tip (Figs. 36, 38–39) straight in lateral view; posterior (lower) sheet projected under frontal (upper) one; posterior



Figures 36–42.—*Dysdera lancerotensis*, right male bulbus. 36, DD frontal; 37, DD frontal of *Dysdera crocota*; 38, DD, external; 39, DD posterior; 40, P external. 41–42, *Dysdera lancerotensis*, spinnerets. 41, Right ALS; 42, Right PLS.

sheet distal internal margin sloped; arch-like ridge present. MA present; hook-like; single pointed projection at internal base. C absent. L absent or hardly visible. LA absent. F absent. AL absent. P (Fig. 40) not fused to T; parallel to T on its proximal part, perpendicular on distal; lateral length from $\frac{1}{3}$ – $\frac{2}{5}$ of T width; ridge present, parallel to T; not expanded; upper margin markedly toothed, on its distal part, very few teeth (1–3); not distally projected; back margin not folded.

Female: (Figs. 32–34, 41, 42). All charac-

ters as in male except: carapace 3.85 long; maximum width 3.22; minimum width 2.38. AME diameter 0.21; PLE 0.18; PME 0.16. Chelicerae 2.03 long; fang long, 1.89. Lengths of female described above: fe1 2.8; pa1 1.72; ti1 2.33; me1 2.33; ta1 0.6; total 9.78; fe2 2.56; pa2 1.49; ti2 2.1; me2 2.19; ta2 0.56; total 8.9; fe3 1.96; pa3 1.16; ti3 1.4; me3 1.91; ta3 0.56; total 7; fe4 2.61; pa4 1.4; ti4 1.86; me4 2.56; ta4 0.65; total 9.08; relative length 1-4-2-3; fe palp 1.86; pa palp 0.83; ti palp 0.79; ta palp 1.26; total 4.74. Spination: palp

Table 2.—Intraspecific spination variability of *Dysdera lancerotensis*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0.1	0	0	1.0.1
Tibia 4 dorsal	0–1.0.1	0–1.0.0	0	0–1.0.1
Tibia 3 ventral	0–1.0–2.0	0	0	0
Tibia 4 ventral	0–1.0–2.0	0	0	0
	Number of rows		Number of spines	
Femur 1 frontal distal		2		0–2
Femur 2 frontal distal		1		0–1
Femur 3 dorsal		0		0
Femur 4 dorsal		2		0–1/0–3

spineless. Fe1 two terminal spines on anterior margin. Fe2 one terminal spine on the anterior margin. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.0.1; distal 1.0.1; ti3v spines arranged in one band: proximal 0.1.0; with two terminal spines. Fe4d spines in one row: 3–2; ti4d spines arranged in two bands: proximal 0.0.1; distal 1.0.1–0; ti4v spines arranged in one band: proximal 0.1.0; with two terminal spines. Dorsal, ventral side of pedipalp covered with hairs, lacking grains.

Abdomen 5.95 long; whitish; cylindrical. Abdominal dorsal hairs 0.054 long; thin, roughly straight, not compressed, blunt, tip enlarged; uniformly, scanty distributed. Vulva (Fig. 32–34) DA clearly distinguishable from VA; DA slightly wider than long; DF narrow in dorsal view. MF margins not fused, poorly developed, membranous. VA rectangular; projected under DA; frontal region with a narrow sclerotized band connecting S attachment to DA; posterior region not sclerotized; AVD absent. Ventral narrow dark bands developed from S attachment. S attached to membranous VA; arms as long as DA, clearly curved; tips not projected; neck as wide as arms. TB usual shape. ALS (Fig. 41) with PS; remaining piriform spigots more external than MS, arranged in three rows; 12 + 1 piriform gland spigots; PMS, PLS (Fig. 42) with 10–15 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 2.81–4.06, female from 2.94–4.69. AME separation ranging from 2/3 diameter to 1. PLE–PME ranging from 1/4 PME diameter to 2/3. Sternum moderately wrinkled. D from markedly larger than B to as large as B. One specimen from La Graciosa has D under groove middle point. P

transversal ridges reduced to two. DA frontal border sometimes straight. S shape somewhat variable. Spination variability in Table 2.

Additional material examined.—**Alegranza:** unknown locality, 3rd week March 1995, 2♂, (P. Oromí, #4115 UB, #2892 UL); unknown date, 1♀; (P. Oromí, #4173 UB). **Fuerteventura:** *La Oliva:* E from Punta Ballena, N from Cotillo; 6 September 1990, 1♀, (H. Enghoff & M. Báez, #2631 ZMK). Cotillo–Los Lagos; 10 February 1997, 1♀, (P. Oromí, 3185 UL). Malpaís de Bayuyo, 20 February 1995; 1♂, (Arnedo, Ribera & Oromí, #2855 UB); 2♀, (Arnedo, Ribera & Oromí, #2856, 4071 UB). *Pájara:* Bco. del Ciervo, Morro de Cavedero N from Morro Jable, Jandía, 4 January 1990, 4♂, (H. Enghoff & M. Báez, #2633–35 ZMK); 1♀, (H. Enghoff & M. Báez, #2632 ZMK); 1juv., (H. Enghoff & M. Báez, #2633 ZMK); 17 February 1995, 2♂, (Arnedo, Ribera & Oromí, #2840, 4057 UB). **La Graciosa:** Caleta del Sebo; 31 March 1996, 1♀, (P. Oromí, 3135 UB). Playa Lambra, 1 April 1996, 1juv., (P. Oromí, 3136 UB). **Lanzarote:** *Haría:* Famara, Mirador del Río, 15 March 1995, 2♂, (unknown, #4103, 4179 UB). *Yaiza:* Montañas de Femés, Atalaya de Femés, 22 February 1995, 2♂, (Arnedo, Ribera & Oromí, #2869, 4092 UB); 1♀, (Arnedo, Ribera & Oromí, #2870 UB). **Montaña Clara:** La Caldera, 23 February 1995, 2♂, (Arnedo, Ribera & Oromí, #2871, 2872 UB); 1juv., (Arnedo, Ribera & Oromí, #4178 UB).

Distribution.—Endemic species from the eastern Canaries.

Dysdera liostethus Simon 1907

Dysdera liostethus Simon 1907: 261, fig. 4E [♂]. (Type lost).

D. clavisetae Wunderlich 1991: 291–292, figs. 24–27 [♂, ♀] (Holotype female; Mirador de Frontera, El Golfo, El Hierro, 8 July 1973, J. Wunderlich leg., not examined. Paratypes; 1♂, Mirador de Frontera, El Golfo, El Hierro, 8 July 1973, J.

Wunderlich leg., #03842, stored at UL, examined. 1♂, MSS Salvador-3, El Hierro, 19 August 1987, A.L. Medina leg., #H-C3-378, stored at UL, examined). —Arnedo et al. 1996: 247–251, figs. 6A–D, 7A–D and 8A–B [♂, ♀]. **New synonymy.**

Distribution.—Widely-spread species in the islands of La Gomera and El Hierro (Wunderlich 1991; Arnedo et al. 1996). Its presence in Lanzarote is considered to be doubtful.

Comments.—The only known material assigned to this species was a male used in the original description (Simon 1907). With the sole exception of *D. lancerotensis*, all male types of the seven Canarian species described by Simon, which were supposed to be stored at MHNH, seem to have been lost (Wunderlich 1987). These type material could not be located either in other museums where Simon's type material from Iberian and north African species (MNCN and BMNH) or other Canarian types (MCNT and UL) were known to be stored. Finally, the late arachnologist Dr. P. Brignoli had been loaned a significant amount of type material from various European museums. Because Dr. Brignoli had published a number of papers on the family Dysderidae, there was a chance that some of Simon's material from the Canaries was in his possession. However, the current curators of his personal collection were unable to locate these specimens.

Most of characters given in the original description of *D. liostethus* are not species-diagnostic for Canarian *Dysdera*. However, the spination pattern is, in this case, very informative. This species is said to share a similar chaetotaxia with *D. rugichelis* Simon 1907. Femora with numerous spines arranged in two asymmetric rows and a strongly spinate posterior tibiae characterize the latter species. This spination pattern is very particular and has only been observed in *D. clavisetae* Wunderlich 1991, *D. enghoffi* Arnedo, Oromí & Ribera 1996, *D. hircuan* Arnedo, Oromí & Ribera 1996, from La Gomera, *D. ratonensis* Wunderlich 1991, from La Palma and *D. verneuui* Simon 1883, from Gran Canaria. *Dysdera verneuui* could be removed from the list because it was described by the same author and a synonymy is very unlikely. *Dysdera ratonensis* and *D. hircuan* are very large species (more than 14 mm in total length), which does not fit with the total length reported for *D. liostethus* (8 mm). Finally, in *D. enghoffi* the

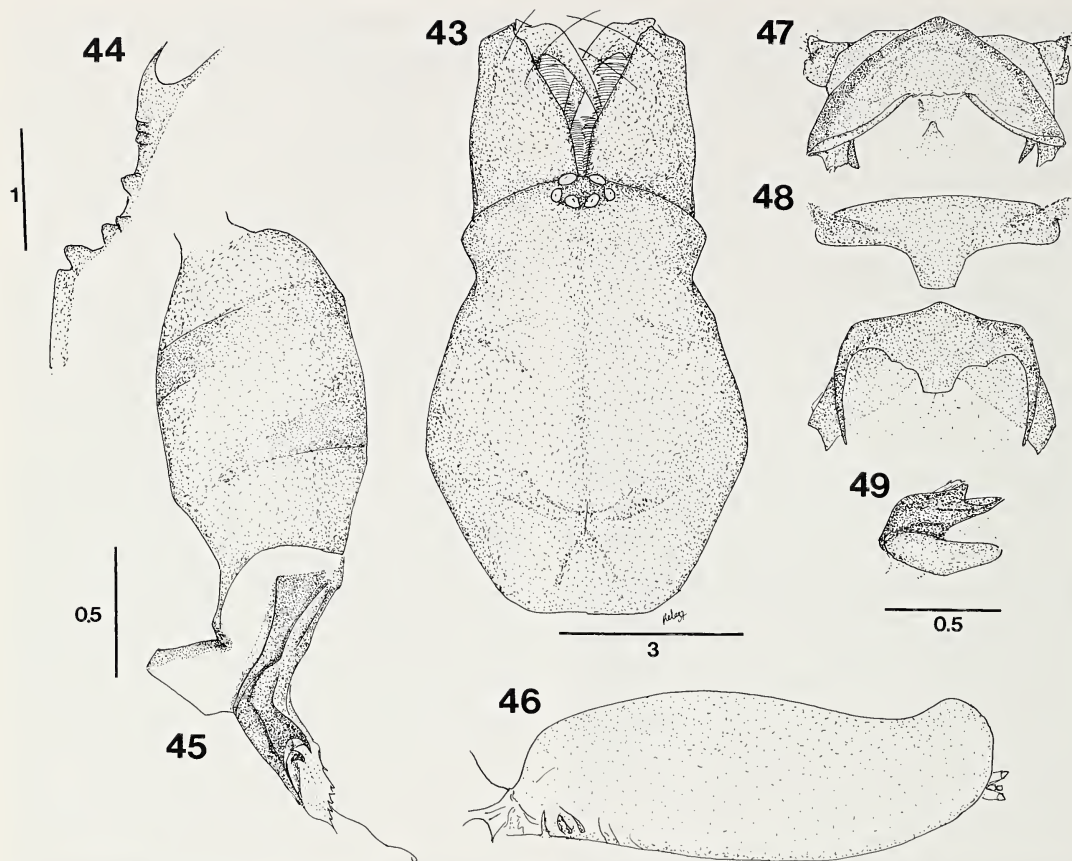
dorsal side of the basal segments of the chelicerae is completely covered with granulations and its copulatory bulbus is characterized by a T and a DD of equal size. In contrast, *D. liostethus* is supposed to have chelicerae in which the basal segment is scarcely covered with granulations, and in the drawing of the male palp, a markedly longer DD than T can be observed. The only remaining species *D. clavisetae* fits these features perfectly. However, there are still two arguments against the synonymy. First, the P of the male bulbus in Simon's drawing is very short while *D. clavisetae* has a long P. However, P development has been shown to be polymorphic in other Canarian endemic *Dysdera*, e.g., *Dysdera macra* Simon 1883 (Arnedo & Ribera 1999). The second problem has to do with the original type locality. However, this argument is not against this synonymy in particular but to any presence of this kind of male genital pattern in the eastern Canaries. The drawing of the male palp of *D. liostethus* suggest a combination of characters that has only been observed in endemic species from the central and western islands. This genitalic pattern is characterized by a tegulum (T) slightly smaller than the distal division (DD), a short but well-developed crest (C), which is located at the DD distal tip, a well-developed lateral sheet (L) with a membranous external lateral border and without apophysis (LA), and a poorly developed AC.

Moreover, additional cases of mistakenly assigned localities in the same article have been demonstrated (Arnedo et al. 1996). Therefore, the original type locality of *D. liostethus* is considered to be doubtful, at least. Finally, a synonymy of both species is considered to be preferable to an unnecessary proliferation of names.

Dysdera longa Wunderlich 1991
Figs. 43–49, 50–53, 54, 55

Dysdera longa Wunderlich 1991: 298, figs. 53–56 [♂, ♀]. (Holotype male; Morro de Cavedero N from Morro Jable, Pájara, Fuerteventura; 4 January 1990; H. Enghoff & M. Báez leg.; #298, stored at ZMK; examined. Paratypes: 1♂, 1♀, 2 juv.; Cumbres de Jandía, Pájara, Fuerteventura; 27 February 1990; P. Oromí leg.; #2710, stored at UL; examined).

Diagnosis.—Very large *Dysdera* similar to remaining eastern species, apart from *D. lan-*



Figures 43–49.—*Dysdera longa*. 43, Carapace, dorsal; 44, Left chelicera, ventral; 45, Right male bulbus, external; 46, Male abdomen, lateral. 47–49, Vulva anterior diverticle: 47, Dorsal; 48, Ventral (S separated); 49, Lateral. Scale bars in mm.

cerotensis, especially in genitalic pattern. Both sexes can be distinguished from the former species by its larger size (carapace length > 6), the dorsal projection of the distal region of the abdomen (mainly in males) (Fig. 46), and the lanceolated hairs not being posteriorly curved. Males have bulb tegulum (T) markedly larger than the distal division (DD) (Fig. 45) and having a sheet-like crest (C) laterally expanded (Fig. 51), while in females the vulva dorsal (DA) and ventral (VA) archs lateral borders are separated (Fig. 49).

Description.—*Male holotype*: (Figs. 43–46, 50–53). Carapace (Fig. 43) 7.07 long; maximum width 5.53; minimum width 3.29. Reddish-orange, frontally darker, becoming lighter towards back; slightly foveate at borders, slightly wrinkled with small black grains mainly at front. Frontal border roughly round, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders convergent; pointed at maximum dor-

sal width, back lateral borders straight; back margin wide, straight. AME diameter 0.36; PLE 0.31; PME 0.25; AME on edge of frontal border, separated from one another by about $\frac{2}{3}$ diameter, close to PLE; PME very close to each other, less than $\frac{1}{4}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum reddish-orange, frontally darker, becoming lighter towards back; very slightly wrinkled, mainly between legs and frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 44) 3.29 long, about $\frac{2}{5}$ of carapace length in dorsal view; fang medium-sized, 2.5; basal segment dorsal, ventral side completely covered with piligerous granulations. Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base, additional ventral tooth on left chelicera; $B > D = M$ (similar); D round,

located roughly at center of groove; B close to basal lamina; M at middle of B and D. Front legs dark orange, back legs yellow. Lengths of male described above: fe1 5.81; pa1 3.91; ti1 6.16; me1 5.81; ta1 1.12; total 22.81; fe2 4.9; pa2 3.5; ti2 4.97; me2 4.55; ta2 1.02; total 18.94; fe3 3.64; pa3 2.33; ti3 3.64; me3 2.59; ta3 0.84; total 13.04; fe4 4.83; pa4 3.03; ti4 4.13; me4 4.69; ta4 1.07; total 17.75; relative length: 1-2-4-3; fe palp 3.49; pa palp 1.63; ti palp 1.77; ta palp 1.63; total 8.52. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.0.0; distal 1.0.1; ti3v spines arranged in one band: proximal 0.0.1; with two terminal spines. Fe4d spines in one row: 13; ti4d spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4v spines arranged in one band: proximal 0.0.1; with two terminal spines. Dorsal, ventral side of pedipalp covered with hairs, lacking grains; very long hairs on back legs as well as on pedipalps. Claws with 8 teeth or less; hardly larger than claw width. Abdomen 11 long; cream-colored; back end projected upwards in lateral view (Fig. 46). Abdominal dorsal hairs 0.108 long; thick, roughly straight, compressed, lanceolate; uniformly, thickly distributed.

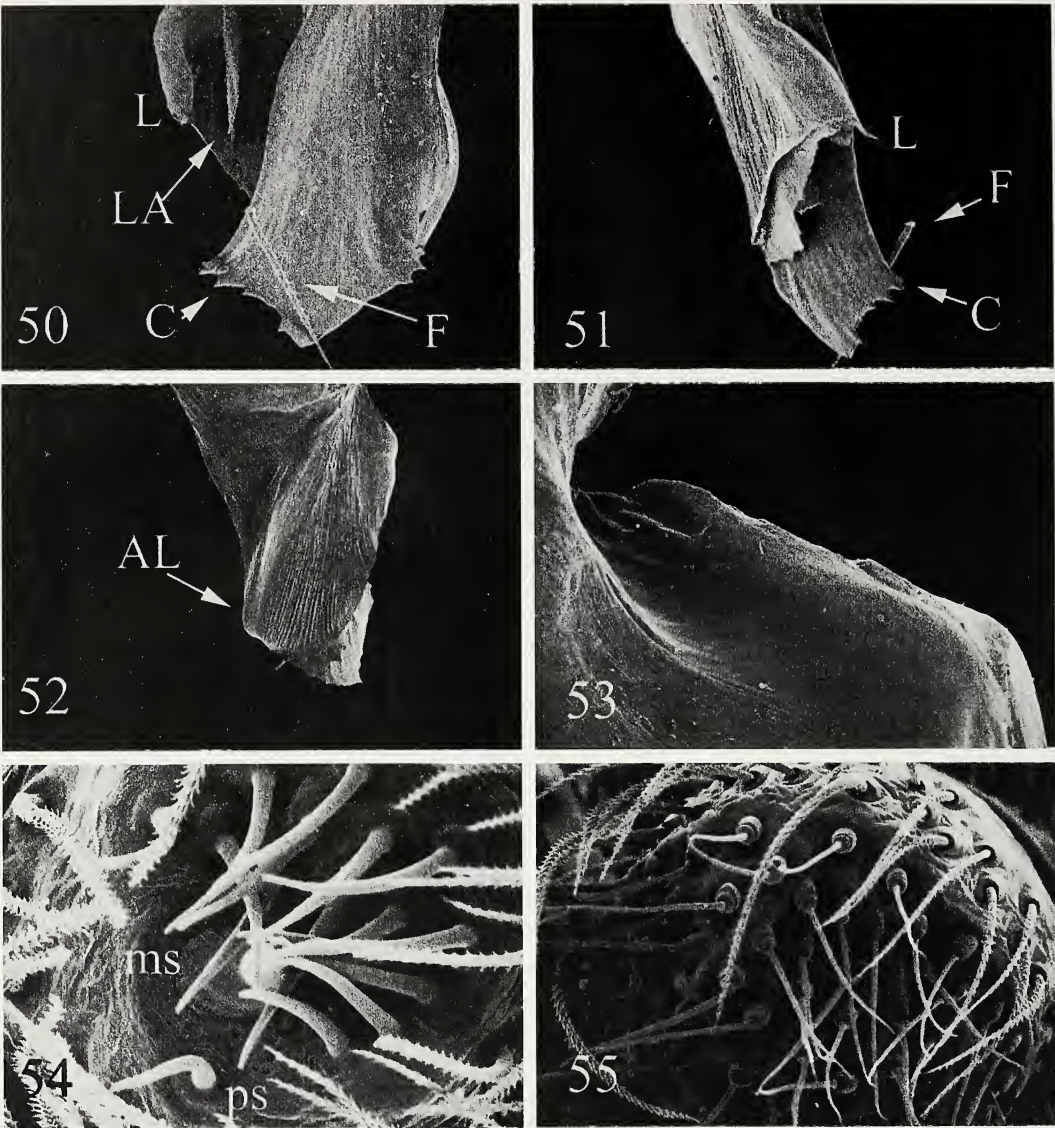
Male copulatory bulbus (Fig. 45) T twice as long as DD; external, internal distal border sloped backwards. DD bent about 45° in lateral view; internal distal border not expanded. ES wider, more sclerotized than IS; IS continuous to tip (slim). DD tip (Figs. 50–52) straight in lateral view. C present, long; distal end beside DD internal tip; distal border truncated, toothed, markedly expanded, projected over DD external part. LF absent. L well-developed; external border sclerotized, laterally markedly folded, distally projected; distal border divergent, continuous. LA present, hook-like; shorter than L. F present, straight, proximally fused to DD. AL present, well-developed, joined to flagellum; proximal border in posterior view smooth, not fused with distal haematodoca. P (Fig. 53) fused to T; perpendicular to T in lateral view; lateral length from ½–⅔ of T width; ridge present, perpendicular to T; distinctly expanded, right-angled; upper margin smooth; not distally projected; back margin not folded.

Female paratype: (Figs. 47–49, 54, 55). All characters as in male except: Carapace 6.79 long; maximum width 5.25; minimum width

3.78. Back lateral borders straight. AME diameter 0.36; PLE 0.32; PME 0.27; AME on edge of frontal border, separated from one another by about ⅔ diameter, close to PLE; PME very close to each other, less than ¼ PME diameter from PLE. Chelicerae 3.12 long; fang medium-sized, 2.9; B > D = M (similar). Legs dark orange-colored. Lengths of female described above: fe1 8.26; pa1 5.6; ti1 7.21; me1 7.21; ta1 1.4; total 29.68; fe2 6.65; pa2 5.18; ti2 6.02; me2 6.02; ta2 1.47; total 25.34; fe3 5.25; pa3 3.15; ti3 3.85; me3 5.04; ta3 1.26; total 18.55; fe4 7; pa4 3.92; ti4 5.6; me4 6.58; ta4 1.75; total 24.85; relative length 1-2-4-3; fe palp 4.9; pa palp 2.66; ti palp 2.1; ta palp 2.8; total 12.46. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.1.0; distal 1.0.1; ti3v spines arranged in one band: proximal 1.0.0; with two terminal spines. Fe4d spines in one row: 11-10; ti4d spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4v spines arranged in one band: proximal 1.0.1; with two terminal spines. Dorsal side of frontal legs covered with small piligerous grains (sparse).

Abdomen 11 long; cream-colored; back end projected upwards in lateral view (slightly). Abdominal dorsal hairs 0.56 long; thick, roughly straight, compressed, lanceolate; uniformly, thickly distributed. Vulva (Figs. 47–49) DA clearly distinguishable from VA; DA slightly wider than long; DF wide in dorsal view. MF margins not fused, well-developed, anterior region sclerotized. VA rectangular, pointed expansion at middle frontal part; projected under DA; frontal region completely sclerotized; posterior region sclerotized at lateral margins; AVD absent. S attachment projected under VA; arms as long as DA, straight; tips not projected; neck as wide as arms. TB usual shape. ALS (Fig. 54) with PS; remaining piriform spigots more external than MS, arranged in two rows; 13 + 1 piriform gland spigots; PMS, PLS (Fig. 55) with more than 20 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 6.30–7.21, female from 6.02–7.35. AME separation from ⅓ diameter to ½. PLE-PME from ⅓ PME diameter to ⅔. Sternum ornamentation sometimes reduced. Relative size of cheliceral teeth variable although no large differences in size. P



Figures 50–55.—*Dysdera longa*, right male bulbus. 50, DD frontal; 51, DD external; 52, DD posterior; 53, P internal. 54–55, *Dysdera longa*, spinnerets. 54, Right ALS; 55, Right PLS.

Table 3.—Intraspecific spination variability of *Dysdera longa*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0–2.0–1	0	0	1.0.0–1
Tibia 4 dorsal	0–1.0.0–1	0	0–1.0.0	0–1.0.0–1
Tibia 3 ventral	1.0–1.0	0	0	0–1.0.0–1
Tibia 4 ventral	0–1.0.0–1	0	0	0
	Number of rows		Number of spines	
Femur 3 dorsal		0		0
Femur 4 dorsal		1		8–13

back margin slightly folded. Spination variability in Table 3.

Additional material examined.—**Fuerteventura:** *Pájara*: Bco. del Ciervo, Cumbres de Jandía, N slope, 17 February 1995, 2♂, (Arnedo, Ribera & Oromí, #2836 UB, 2838 UL); 7♀, (Arnedo, Ribera & Oromí, #2837, 3183 UL, 4054–56, 4058, 4117 UB); 10juv., (Arnedo, Ribera & Oromí, #2831–35, 2839, 4050–53 UB); 27 February 1990, 1♀, (P. Oromí, #2621 MCNT).

Distribution.—Endemic species from the Jandía peninsula, at southern Fuerteventura.

Dysdera nesioties Simon 1907

Figs. 56–63, 64–67, 68, 69

Dysdera nesioties Simon 1907: 260–261, fig. 4G [♂] (Type lost).—Reimoser 1919: 200.—Denis 1963: 37–38.—Schmidt 1973: 360–361.—Rambla 1978: 132–133.—Arnedo et al. 1996.

Dysdera wollastoni Blackwall 1864 nec. Kulczynski 1899: 23–26, fig. 22–24 [♂].—Reimoser 1919: 200.—Berland & Denis 1946: 224. Wunderlich 1991: 312, Fig. 129 [♂]

Dysdera wollastoni nesioties Simon 1912: 59–60.—Denis 1941: 108.

Types.—Neotypes, by present designation, 1♂, 1♀, 3juv.; label states: “*Dysdera wollastoni* Blackwall, Ins. Salvages (Garreta leg.)”; #B 536 (jar number), stored at MHNP.

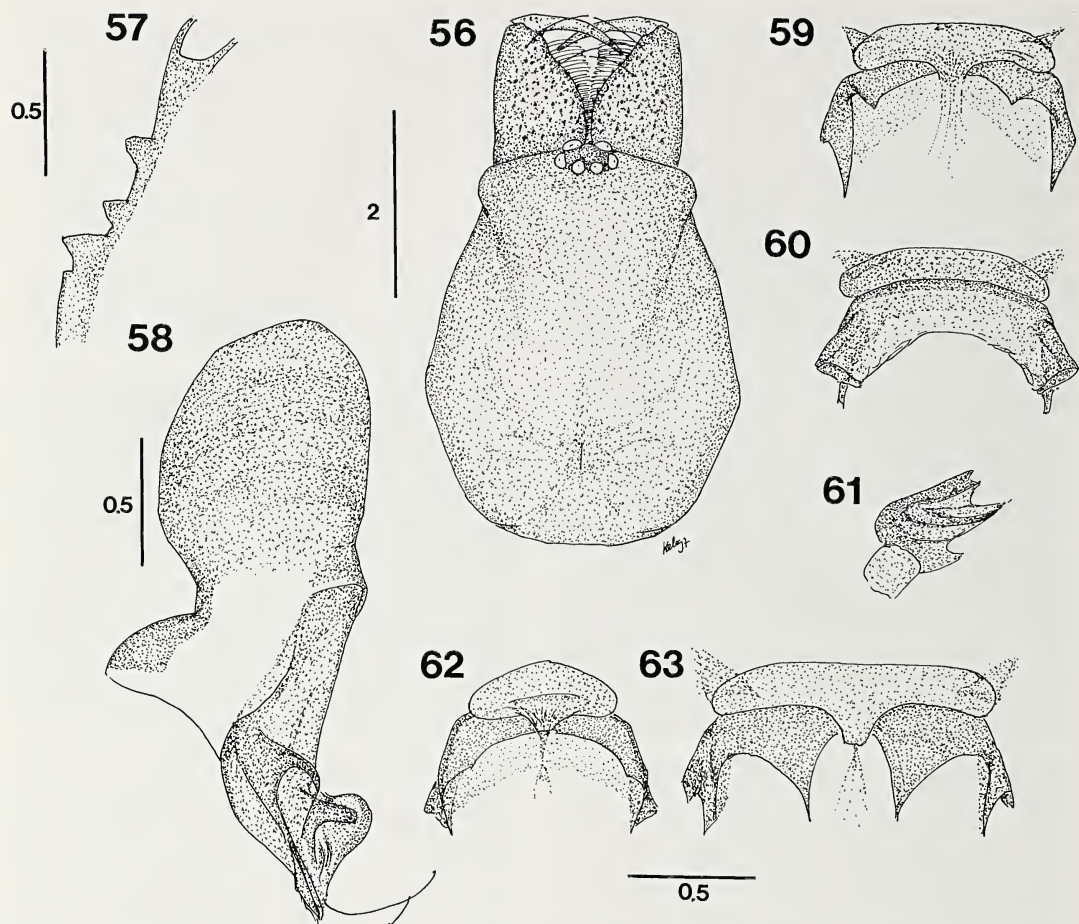
Diagnosis.—This species strongly resembles *D. spinidorsum*. Males can be distinguished from the latter by the short lateral apophysis (LA) (Fig. 64), the moderately expanded crest (C) (Fig. 65), and the presence of a fold between the additional lateral sheet (AL) and the flagellum (F) (Fig. 66). Female vulva has the backwards projection of the medial fold (MF) not so well developed (Fig. 59) and displays posterior sclerotization of the ventral arch (VA) (Fig. 60).

Description.—**Male neotype:** (Figs. 56–58, 64–67). Carapace (Fig. 56) 4.23 long; maximum width 3.71; minimum width 2.2. Dark brownish-orange, frontally darker, becoming lighter towards back; smooth with some small black grains mainly at front. Frontal border roughly triangular, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders convergent; rounded at maximum dorsal width point, back lateral borders straight; back margin wide, straight. AME diameter 0.27; PLE 0.21; PME 0.18; AME on edge of frontal border, separated from one another by about $\frac{2}{3}$ diameter, close to PLE; PME very close to each other, about

$\frac{1}{3}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum orange, frontally darker, becoming lighter towards back; very slightly wrinkled, mainly between legs and frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 57) 1.82 long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-sized, 1.05; basal segment dorsal, ventral side completely covered with piligerous granulations. Chelicera inner groove short, about $\frac{1}{3}$ cheliceral length; armed with three teeth and lamina at base; $D = B > M$ (similar); D round, located roughly at centre of groove; B close to basal lamina; M at middle of B and D. Front legs dark orange, back legs yellow. Lengths of male described above: fe1 3.5; pa1 2.45; ti1 3.5; me1 3.29; ta1 0.63; total 13.37; fe2 3.08; pa2 2.1; ti2 2.8; me2 2.94; ta2 0.7; total 11.62; fe3 3.26; pa3 1.4; ti3 1.75; me3 2.17; ta3 0.7; total 9.28; fe4 3.29; pa4 1.68; ti4 2.7; me4 3.15; ta4 0.7; total 11.52; relative length: 1-2-4-3; fe palp 2.1; pa palp 1.12; ti palp 1.13; ta palp 1.13; total 5.48. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.0.1; distal 1.0.1; ti3v spines arranged in two bands: proximal 1.0.0; distal 1.0.0; with two terminal spines. Fe4d spines in two rows: anterior 4; posterior 6–7; ti4d spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4v spines arranged in two bands: proximal 1.0.1; distal 0-1.0.0-1; with two terminal spines. Dorsal side of frontal legs covered with small piligerous grains; ventral side covered with hairs, lacking grains; very long hairs on back legs as well as on pedipalps. Claws with 8 teeth or less; hardly larger than claw width. Abdomen 6.86 long; whitish; cylindrical. Abdominal dorsal hairs 0.11 long; thick, roughly straight, compressed, lanceolate; uniformly, thickly distributed.

Male copulatory bulbus (Fig. 58) T as long as DD; external, internal distal border sloped backwards. DD bent about 45° in lateral view; internal distal border markedly expanded. ES wider, more sclerotized than IS; IS continuous to tip (diffused). DD tip (Figs. 64–67) straight in lateral view; frontal (upper) sheet internal part markedly projected above posterior (lower) sheet. C present, long; distal end beside DD internal tip; distal border rounded, smooth, markedly expanded, perpendicular to

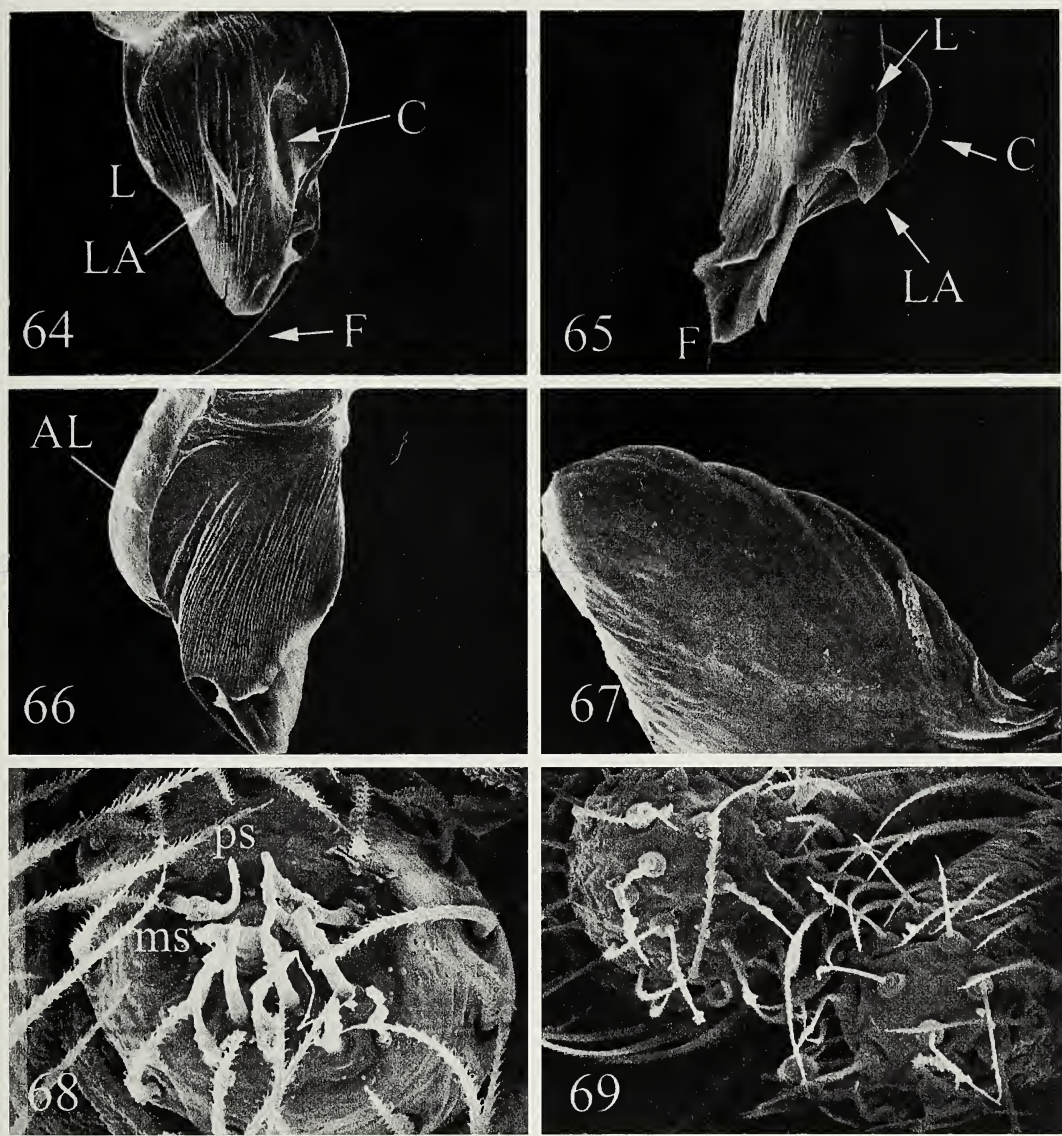


Figures 56–63.—*Dysdera nesiotetes*. 56, Carapace, dorsal; 57, Left chelicera, ventral; 58, Right male bulbus, external. 59–63, Vulva anterior diverticle: 59, Dorsal; 60, Ventral; 61, Lateral. 62, 63, Variability, ventral. Scale bars in mm.

DD. LF absent. L well-developed; external border sclerotized, laterally markedly folded; distal border divergent, continuous. LA present, hook-like; shorter than L. F present, tip bent backwards, proximally fused to DD. AL present, well-developed, not joined to flagellum; proximal border in posterior view smooth, not fused with distal haematodoca. P (Fig. 67) fused to T; perpendicular to T in lateral view; lateral length from $\frac{1}{2}$ – $\frac{2}{3}$ of T width; ridge present, perpendicular to T; distinctly expanded, rounded; upper margin slightly toothed, mainly on external side, along its extent, few teeth (4–6); not distally projected; back margin not folded.

Female: (Figs. 60, 61, 68, 69). All characters as in male except: carapace 4.55 long; maximum width 3.71; minimum width 2.38.

AME diameter 0.27; PLE 0.21; PME 0.18; AME separated from one another by about $\frac{2}{5}$ diameter. Chelicerae 1.92 long; fang medium-sized, 1.19. $B > D > M$ (similar). Front legs dark orange, back legs yellow. Lengths of female described above: fe1 3.36; pa1 2.38; ti1 2.94; me1 2.8; ta1 0.63; total 12.11; fe2 3.86; pa2 2.1; ti2 2.66; me2 2.66; ta2 0.63; total 11.91; fe3 2.24; pa3 1.4; ti3 1.75; me3 2.31; ta3 0.63; total 8.33; fe4 3.5; pa4 1.68; ti4 2.66; me4 3.22; ta4 0.7; total 11.76; relative length 1-2-4-3; fe palp 2.2; pa palp 0.98; ti palp 0.84; ta palp 1.19; total 5.21. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.0.1; distal 1.0.0; ti3v spines arranged in two bands: proximal 1.0.0; distal 1-0.0.0; with two terminal spines. Fe4d spines in two rows: ante-



Figures 64–69.—*Dysdera nesiotes*, right male bulbus. 64, DD frontal; 65, DD external; 66, DD posterior. 67, P external. 68–69, *Dysdera nesiotes*, spinnerets. 68, Right ALS; 69, Right PMS (lower) and PLS (upper).

rior 1; posterior 6-5; ti4d spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4v spines arranged in two bands: proximal 1.0.1; distal 1-2.0.0-1; with two terminal spines.

Abdomen 6.86 long; whitish; cylindrical. Abdominal dorsal hairs 0.126 long; thick, roughly straight, compressed, lanceolate; uniformly, thickly distributed. Vulva (Fig. 60, 61) DA not distinguishable from VA; rectangular; DA twice as wide as long; DF wide in dorsal view. MF well-developed, completely sclero-

tized, projected backwards, shorter than DA lateral length. VA frontal region completely sclerotized; posterior region sclerotized in most anterior area; tooth-shaped expansion from internal back border; not joined to lateral sclerotization, about half of DF lateral margins; AVD absent. S attachment not projected under VA; arms as long as DA, slightly curved; ends projected forwards; neck hardly visible. TB usual shape. ALS (Fig. 68) with PS; remaining piriform spigots more external

Table 4.—Intraspecific spination variability of *Dysdera nesiotés*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.0–2.0–1	0	0	1.0.0–1
Tibia 4 dorsal	0–1.0.1	0	0	0–1.0.1
Tibia 3 ventral	0–2.0.0–1	0	0	0–1.0.0
Tibia 4 ventral	0–1.0–1.0–1	0	0	0–1.0.0–1
	Number of row			Number of spines
Femur 3 dorsal		0–1		0–2
Femur 4 dorsal		2		1–6/4–7

than MS, arranged in two rows; 10 + 1 piri-form gland spigots; PMS, PLS (Fig. 69) with 10–15 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 3.64–4.48, female from 3.92–5.46. AME separation from 1/3 diameter to 1/5. PLE-PME from 1/3 PME diameter to 1/2. In general, B largest, D clearly above groove middle point and M position variable. Some female specimens have abdominal hairs that are not clearly lanceolated. An unusual range of variability in DA shape can be observed. Two extreme types can be recognized although several intermediate forms have been recorded. The first of them (Fig. 62) is distinguished by a markedly wide DA in dorsal view, with rectangular anterior lateral borders, tooth-like ventral sclerotization which is restricted to the frontal region, and S as long as DA. The second one (Fig. 63) shows a moderately wide DA, with its anterior frontal margins rounded, more developed sclerotization of the frontal region with tooth-like projection hardly noticeable, and S markedly shorter than DA. Female specimens from the Selvagens Islands as well as a single specimen from northeastern Lanzarote fit the first type, while the second one is spread over the remaining localities. Spination variability in Table 4.

Additional material examined.—**Alegranza:** unknown locality, 3rd week March 1995, 1♂, (P. Oromí, #2890 UB); 3♀, (P. Oromí, #2891, 4109, 4107 UB). **Lanzarote:** *Haria:* Malpaís de la Corona, Charcos de marea, 25 February 1995, 1♂, (Arnedo, Ribera & Oromí, 2887 UB). Montañas de Famara, around Mirador de Haría; 22 February 1995, 1♂, (Arnedo, Ribera & Oromí, 2866 UB); 1♀, (Arnedo, Ribera & Oromí, 4087 UB). Montañas de Famara, around Mirador del Río, 22 February 1995; 6♂, (Arnedo, Ribera & Oromí, #2861, 2863, 4072–3 UL, 4075, 4077 UB); 7♀, (Arnedo, Ribera

& Oromí, #2857, 2860, 2862 UL, 2936, 4082, 4084–5 UB). *Yaiza:* Montañas de Femés, Atalaya de Femés, 1♂, 22 February 1995, (Arnedo, Ribera & Oromí, 2868 UB); 1♀, (Arnedo, Ribera & Oromí, 2867 UB). **Montaña Clara:** La Caldera, 23 February 1995, 4♂, (Arnedo, Ribera & Oromí, #2873, 2878, 2888–9 UB); 8♀, (Arnedo, Ribera & Oromí, #2818, 2874, 2876, 2879, 2880, 4093–95 UB). **Ilhas Selvagens:** 3♂, 1♂ subad., 1♀, 1juv.; label states: “*Dysdera verneau* Simon, Grant coll.”; #BM1897.10.18.41–46 BMNH.

Distribution.—This species is spread over Lanzarote, the northern islets and the Selvagens Islands.

Comments.—The male type material of this species, which is the only type known since the females were found to be a wrong identification (Arnedo & Ribera 1999), has been lost. Comments for *D. liostethus* are equally applicable to this species. Due to the taxonomic confusion that has surrounded *D. nesiotés*, and according to article 75 of the ICZN (4th edition), a neotype was designated. The neotype was selected from a series of specimens studied by Simon (a label stating this is included in the specimen’s vial), the original author of *D. nesiotés*. Simon identified these specimens as *D. wollastoni* sensu Kulczynski 1899, which was, subsequently, considered a junior synonym of *D. nesiotés* (Denis 1963). The locality of the neotypes does not match the original type locality. However, the last is considered to be doubtful (see discussion below).

Before the present study, it was suggested that *D. nesiotés* was present in the Canarian islands of La Palma and Tenerife and in the Selvagens Islands, a group of three islets located between Madeira and the Canaries about 150 km north of Tenerife. Nevertheless, no specimens assigned to this species have ever

been reported from La Palma or Tenerife after the original description (Simon 1907). The supposed presence of this species in Tenerife could be explained by a misidentification. Simon transferred three females, originally assigned to *Dysdera insulana* Simon 1883, to *D. nesiotes*. After examination of these females by us, they turned out to belong to the species *Dysdera propinqua* Ribera, Ferrández & Blasco 1986 (Arnedo & Ribera 1999). The latter species is widely distributed in Tenerife. Probably, this locality was erroneously assigned after misidentification of additional labeled female material. The presence of *D. nesiotes* in La Palma is even more difficult to explain. However, other cases of possible wrongly assigned localities have been proposed in other Canarian *Dysdera* described by Simon, e.g., the presence of *D. insulana* in La Palma and Lanzarote (Arnedo & Ribera 1997). Moreover, the geographical distribution of certain morphological characters (e.g., the presence of LA and F is restricted to endemic species from the eastern Canaries), give support to the absence of *D. nesiotes* from the western and central Canaries.

Dysdera wollastoni Blackwall 1864 was considered a junior synonym of *D. crocata* by Denis (1963), based on revision of the type material. Recently, Wunderlich (1991) has rejected this synonymy based solely on the fact that *D. crocata* is so well known that it would be unlikely that a trained arachnologist would commit such mistake. However, Wunderlich himself has described a new Canarian endemism that was subsequently synonymized with *D. crocata* (Arnedo & Ribera 1999). In any case, Blackwall's actual description corresponds to *D. crocata*. Kulczynski (1899) published a thorough and nicely illustrated redescription of what he wrongly identified as *D. wollastoni*, based on specimens also collected in the Selvagens. This redescription was similar to Simon's original description of *D. nesiotes* (Simon 1883) to such an extent that Simon subsequently considered *D. nesiotes* as a subspecies of *D. wollastoni* (Simon 1912). Lately, Denis (1963) claimed to have found no morphological evidence to justify a subspecies status for the Canarian specimens, and, because Kulczynski's redescription was based on a wrong identification, *D. nesiotes* was the senior synonym. Recently, Wunderlich (1991) has considered that the synonymy

of *D. wollastoni* and *D. nesiotes* is also based on a misidentification. Nevertheless, we have been unable to find any diagnostic difference between the studied populations of *D. nesiotes* from the Selvagens Islands and those from the eastern Canaries, and thus we consider them as allopatric populations of the same species.

Dysdera sanborondon new species

Figs. 70–75, 76–79, 80, 81

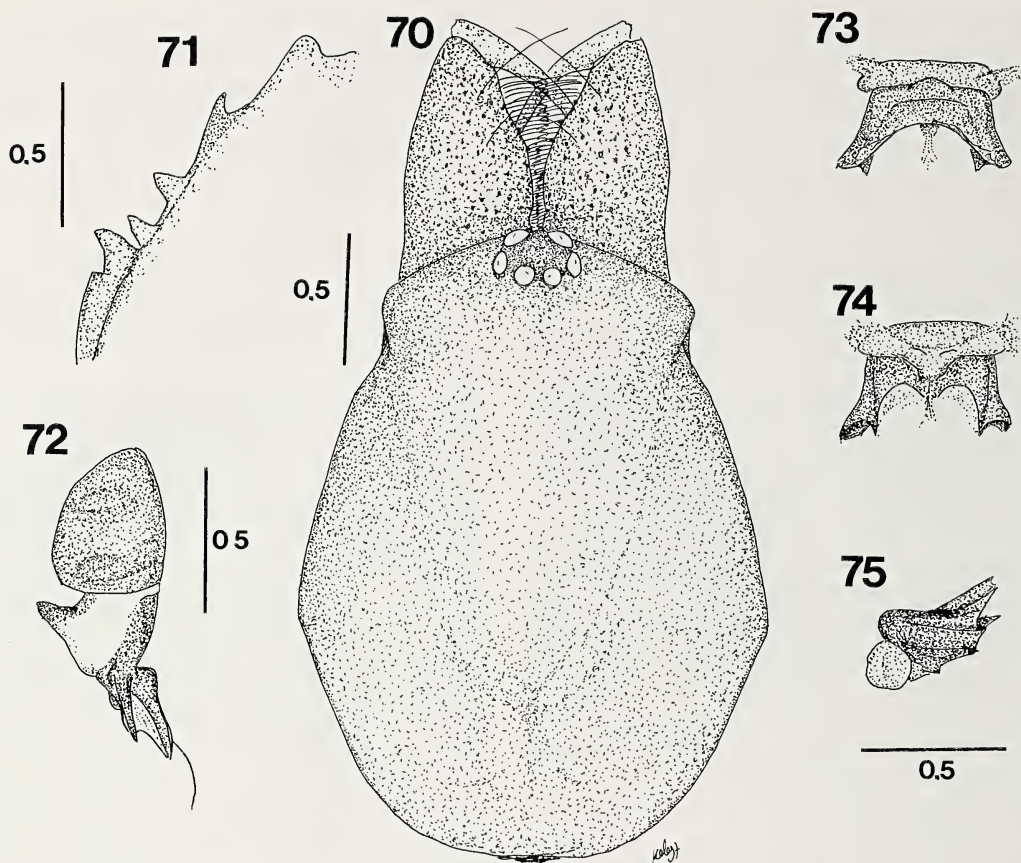
Types.—Holotype male from Montañas de Tegú, Betancuria, Fuerteventura; 18 February 1995, (Arnedo, Ribera & Oromí, #2850 UB). Paratype female from Cuchillos de Jacomar, between Valle de Jacomar and Valle de los Toneles, Tuineje, Fuerteventura; 19 February 1995, (Arnedo, Ribera & Oromí, #2852 UB).

Etymology.—The name in apposition of this species refers to San Borondón, the fantasy island that the first Spanish settlers of the 15th and 16th centuries believed they saw from the Canaries on extremely clear days.

Diagnosis.—Very small *Dysdera* (carapace length < 3). Even though this species shows a similar genitalic pattern to the remaining eastern species (with the exception of *D. lancerotensis*) both sexes can be easily distinguished by its smaller size and lack of lanceolate abdominal hairs. Males have neither lateral sheet apophysis (LA) (Fig. 76) nor additional lateral sheet (AL) (Fig. 78), and in females, the posterior region of the ventral arch (VA) is markedly sclerotized (Fig. 74).

Description.—*Male holotype:* (Figs. 70–72, 76–79). Carapace (Fig. 70) 2.33 long; maximum width 1.72; minimum width 1.12. Uniformly dark brownish-orange, heavily wrinkled, foveate, covered with small black grains. Frontal border roughly triangular, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders convergent; rounded at maximum dorsal width point, back lateral borders straight; back margin narrow, straight. AME diameter 0.16; PLE 0.14; PME 0.11; AME on edge of frontal border, separated from one another by less than $\frac{1}{4}$ diameter, close to PLE; PME very close to each other, less than $\frac{1}{4}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; as long as wide at base; semicircular groove at tip. Sternum dark orange, uniformly distributed; wrinkled; uniformly covered in slender black hairs.

Chelicerae (Fig. 71) 1.09 long, about $\frac{1}{3}$ of carapace length in dorsal view; fang medium-

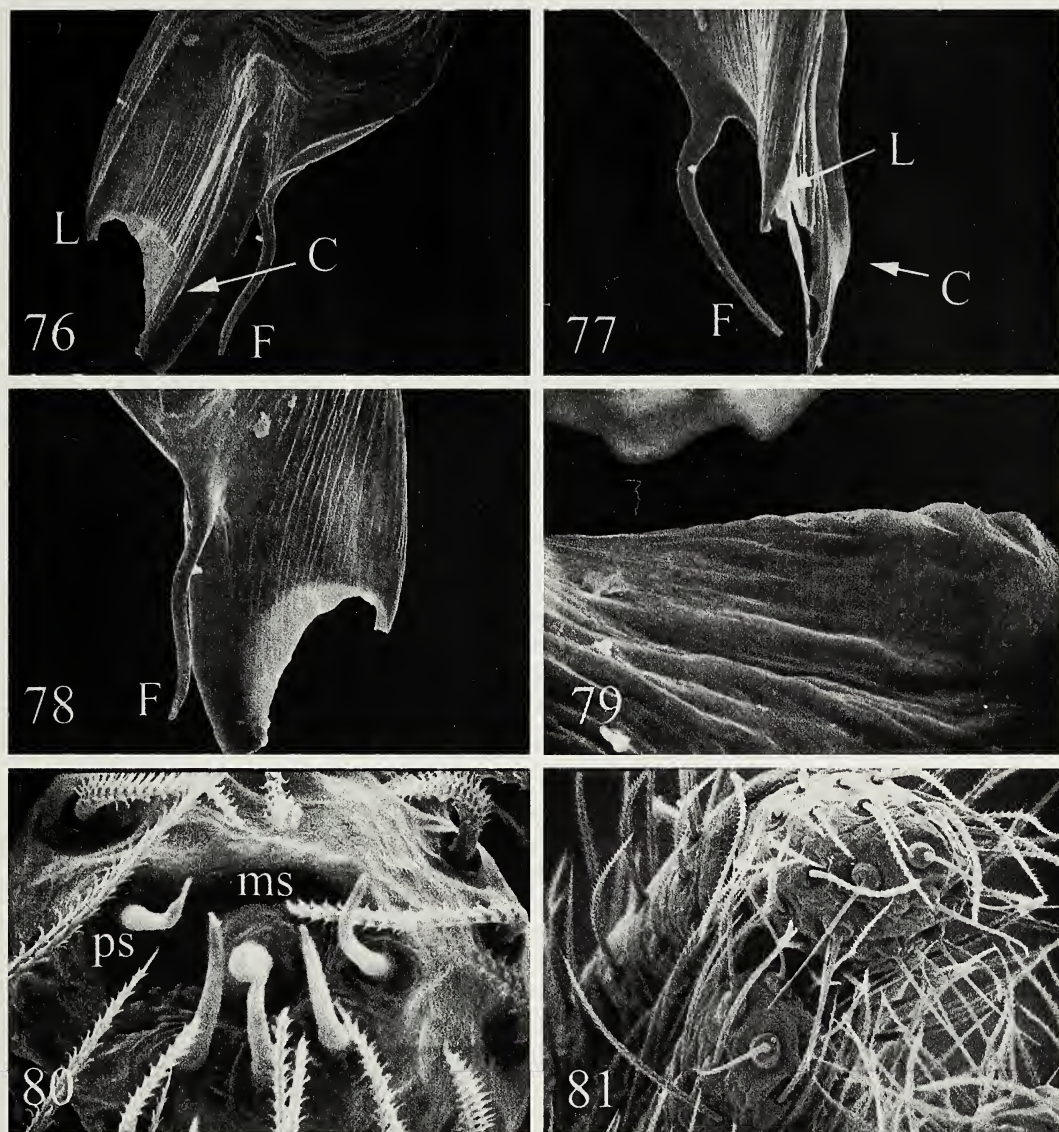


Figures 70-75.—*Dysdera sanborondon* new species. 70, Carapace, dorsal; 71, Left chelicera, ventral; 72, Right male bulbus, external. 73-75, Vulva anterior diverticle: 73, Dorsal; 74, Ventral; 75, Lateral. Scale bars in mm.

sized, 0.74; basal segment dorsal, ventral side completely covered with piligerous granulations. Chelicera inner groove medium-size, about $\frac{2}{3}$ cheliceral length; armed with three teeth and lamina at base; D = B > M (similar); D triangular, located roughly at center of groove; B close to basal lamina; M at middle of B and D. Legs orange. Lengths of male described above: fe1 1.86; pa1 1.16; ti1 1.54; me1 1.44; ta1 0.42; total 6.42; fe2 1.54; pa2 1.02; ti2 1.35; me2 1.35; ta2 0.42; total 5.68; fe3 1.26; pa3 0.7; ti3 0.84; me3 1.12; ta3 0.32; total 4.24; fe4 1.77; pa4 0.88; ti4 1.4; me4 1.63; ta4 0.42; total 6.1; relative length: 1-4-2-3; fe palp 0.93; pa palp 0.51; ti palp 0.46; ta palp 0.56; total 2.46. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.0.1; distal 1.0.0; ti3v spines arranged in one band: proximal 1.0.0; with two terminal spines. Fe4d

spines in two rows: anterior 1; posterior 2; ti4d spines arranged in two bands: proximal 1.0.1; distal 0.0.1; ti4v spines arranged in one band: proximal 1.0.1; with two terminal spines. Dorsal side of frontal legs covered with small piligerous grains; ventral side covered with hairs, lacking grains. Claws with 8 teeth or less; hardly larger than claw width. Abdomen 2.4 long; whitish. Abdominal dorsal hairs 0.027 long; medium thickness, roughly straight, not compressed, blunt, tip not enlarged; uniformly, thickly distributed.

Male copulatory bulbus (Fig. 72) T slightly smaller than DD; external distal border straight; internal sloped backwards. DD bent about 45° in lateral view; internal distal border markedly expanded. ES wider, more sclerotized than IS; IS continuous to tip (slim). DD tip (Fig. 76-78) straight in lateral view. C present, long; distal border rounded, smooth,



Figures 76–81.—*Dysdera sanborondon* new species, right male bulbus. 76, DD external; 77, DD frontal; 78, DD posterior; 79, P internal. 80–81, *Dysdera sanborondon* new species, spinnerets. 80, Right ALS; 81, Right PMS (lower) and PLS (upper).

slightly expanded, perpendicular to DD. LF absent. L well-developed; external border sclerotized, not folded, distally projected; distal border divergent, continuous. LA absent. F present, distally curved to external side, not fused to DD. AL absent. P (Fig. 79) fused to T; markedly sloped on its proximal part, perpendicular on distal; lateral length from $\frac{1}{2}$ – $\frac{2}{3}$ of T width; ridge present, perpendicular to T; not expanded; upper margin markedly toothed, on its distal part, few teeth (4–6); not distally projected; back margin not folded.

Female paratype: (Figs. 73–75, 80, 81). All characters as in male except: Carapace 2.79 long; maximum width 2.05; minimum width 1.35. AME diameter 0.16; PLE 0.16; PME 0.12.

Chelicerae 1.3 long; fang medium-sized, 0.93; basal segment dorsal, ventral side completely covered with piligerous granulations (distally slightly reduced). $B > D = M$ (similar). Legs yellow. Lengths of female described above: fe1 2; pa1 1.35; ti1 1.68; me1 1.68; ta1 0.39; total 7.1; fe2 1.77; pa2 1.26;

ti2 1.63; me2 1.63; ta2 0.42; total 6.71; fe3 1.49; pa3 0.84; ti3 0.98; me3 1.35; ta3 0.42; total 5.08; fe4 2.1; pa4 1.02; ti4 1.49; me4 1.86; ta4 0.42; total 6.89; relative length 1-4-2-3; fe palp 1.12; pa palp 0.6; ti palp 0.51; ta palp 0.7; total 2.93. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.0.1; distal 1.0.0; ti3v spines arranged in one band: proximal 1.0.1; with two terminal spines. Fe4d spines in one row: 2; ti4d spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4v spines arranged in two bands: proximal 1.0.1; medial-proximal 0.0.1; with two terminal spines. Abdomen 6.8 long; whitish; cylindrical. Abdominal dorsal hairs 0.063 long; thin, curved, compressed, pointed; uniformly, thickly distributed.

Vulva (Fig. 73–75) DA not distinguishable from VA; rectangular, pointed expansion at middle frontal part; DA slightly wider than long; DF wide in dorsal view. MF margins not fused, well-developed, completely sclerotized. VA frontal region completely sclerotized; posterior region sclerotized at lateral margins; AVD absent. S attachment projected under VA; arms as long as DA, straight; tips not projected; neck as wide as arms. TB usual shape. ALS (Fig. 80) with PS; remaining piriform spigots more external than MS, arranged in one row; 4 + 1 piriform gland spigots; PMS, PLS (Fig. 81) with 5–10 aciniform gland spigots.

Intraspecific variation.—Unknown.

Distribution.—Endemic species from central Fuerteventura.

Dysdera spinidorsum Wunderlich 1991

Figs. 82–87, 88–91, 92, 93

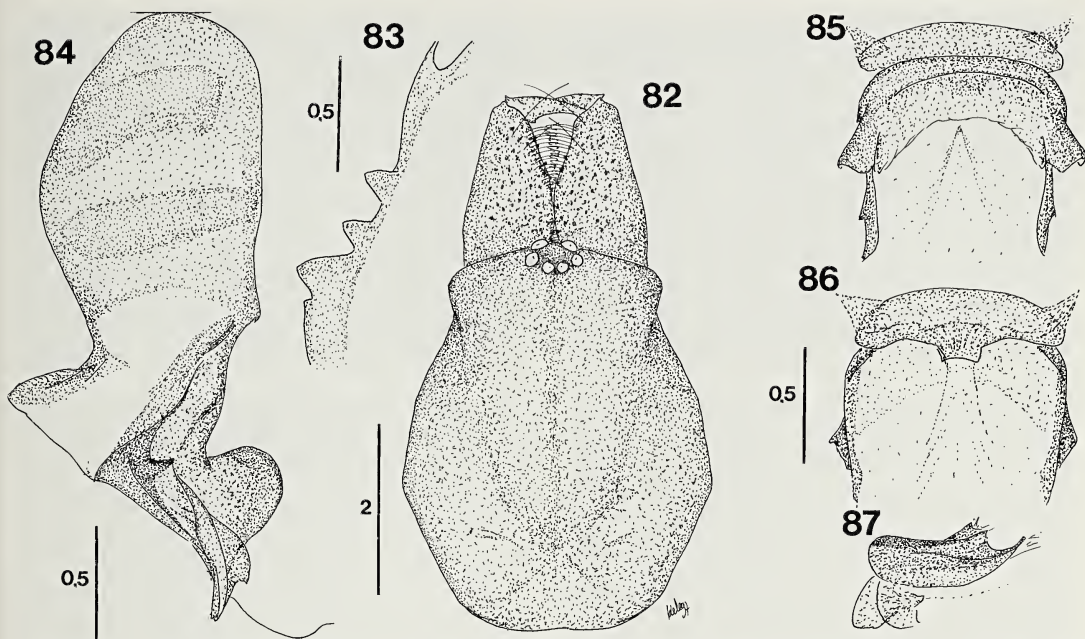
Dysdera spinidorsum Wunderlich 1991: 307–308, figs. 101–102 [♀]. (Holotype female; NE road to Betancuria (550 m), Betancuria, Fuerteventura; 5 January 1990; H. Enghoff, M. Báez, ♀, leg.; #307, stored at ZMK; examined.)

Diagnosis.—Both sexes of this species can be distinguished from the sympatric *D. sanborondon* by its larger size (carapace length > 4) and lanceolate abdominal hairs. Males display both a well-developed lateral sheet apophysis (LA) (Fig. 88) and additional lateral sheet (AL) (Fig. 90). In females, the posterior region of the ventral arch (VA) is membranous (Fig. 86). Males differ from the morphologically closely related *D. nesiotetes* by having

the tegulum (T) longer than the distal division (DD) (Fig. 84), the lateral sheet apophysis (LA) being frontally projected (Fig. 88) and the crest (C) distinctly expanded (Fig. 89). In females, the medial fold (MF) is markedly projected backwards (Fig. 85) and the ventral arch (VA) shows a reduction of its ventral sclerotization (Fig. 86).

Description.—*Male*: (Figs. 82–84, 88–91). Carapace (Fig. 82) 4.9 long; maximum width 3.64; minimum width 2.59. Reddish-orange, frontally darker, becoming lighter towards back; slightly foveate at borders, slightly wrinkled with small black grains mainly at front. Frontal border roughly triangular, from $\frac{1}{2}$ – $\frac{3}{5}$ carapace length; anterior lateral borders convergent; pointed at maximum dorsal width, back lateral borders straight; back margin wide, straight. AME diameter 0.23; PLE 0.22; PME 0.17; AME on edge of frontal border, separated from one another by about $\frac{2}{3}$ diameter, close to PLE; PME very close to each other, about $\frac{1}{3}$ PME diameter from PLE. Labium trapezoid-shaped, base wider than distal part; longer than wide at base; semicircular groove at tip. Sternum orange-yellow, frontally darker, becoming lighter towards back; very slightly wrinkled, mainly between legs and frontal border; uniformly covered in slender black hairs.

Chelicerae (Fig. 83) 2.1 long, about $\frac{2}{5}$ of carapace length in dorsal view; fang medium-sized, 1.4; basal segment dorsal, ventral side completely covered with piligerous granulations. Chelicera inner groove medium-size, about $\frac{2}{5}$ cheliceral length; armed with three teeth and lamina at base; B > D = M (similar); D round, located roughly at center of groove; B close to basal lamina; M at middle of B and D. Legs yellow. Lengths of male described above: fe1 3.82; pa1 2.56; ti1 3.82; me1 3.49; ta1 0.74; total 14.43; fe2 3.49; pa2 2.37; ti2 3.35; me2 3.21; ta2 0.84; total 13.26; fe3 2.7; pa3 1.58; ti3 1.86; me3 2.51; ta3 0.74; total 9.39; fe4 3.45; pa4 1.96; ti4 2.65; me4 3.4; ta4 0.79; total 12.25; relative length: 1-2-4-3; fe palp 2.1; pa palp 1.16; ti palp 0.93; ta palp 1.12; total 5.31. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.2.1; distal 1.0.1; ti3v spines arranged in two bands: proximal 1.0.1-0; distal 1-0.0.0; with two terminal spines. Fe4d spines in two rows: anterior 1; posterior 5; ti4d spines arranged in two bands:



Figures 82–87.—*Dysdera spinidorsum*. 82, Carapace, dorsal; 83, Left chelicera, ventral; 84, Right male bulbus, external; 85–87, Vulva anterior diverticle: 85, Dorsal; 86, Ventral; 87, Lateral. Scale bars in mm.

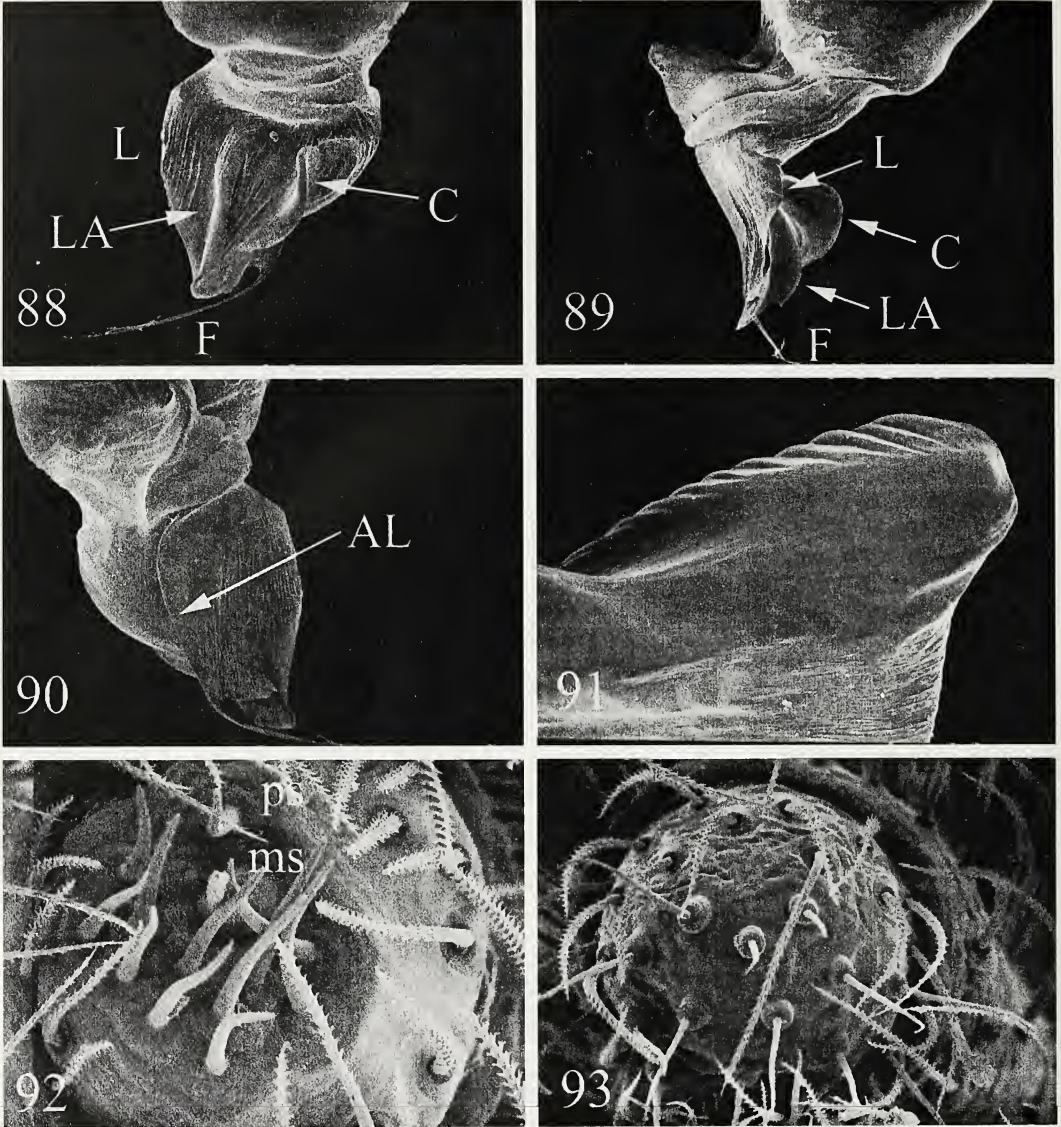
proximal 0.0.1; distal 0.0.1; ti4v spines arranged in two bands: proximal 0–1.0.1; distal 0–1.0.0; with two terminal spines. Dorsal side of frontal legs covered with small piligerous grains; ventral side covered with hairs, lacking grains; very long hairs on back legs as well as on pedipalps. Claws with 8 teeth or less; hardly larger than claw width. Abdomen 4.9 long; cream-colored; cylindrical. Abdominal dorsal hairs 0.2 long; thick, roughly straight, compressed, lanceolate; uniformly, thickly distributed.

Male copulatory bulbus (Fig. 84) T slightly longer than DD; external, internal distal border sloped backwards. DD bent about 45° in lateral view; internal distal border markedly expanded. ES wider, more sclerotized than IS (slightly); IS continuous to tip (diffuse). DD tip (Fig. 88–90) straight in lateral view; frontal (upper) sheet internal part markedly projected above posterior (lower) sheet. C present, long; distal end beside DD internal tip; distal border rounded, smooth, markedly expanded, perpendicular to DD. LF absent. L well-developed; external border sclerotized, laterally markedly folded; distal border divergent, continuous. LA present, sheet-like; as long as L, completely fused. F present, tip divided, proximally fused to DD. AL present,

well-developed, joined to flagellum; proximal border in posterior view smooth, not fused with distal haematodoca. P (Fig. 91) fused to T; perpendicular to T in lateral view; lateral length from $\frac{1}{2}$ – $\frac{2}{3}$ of T width; ridge present, perpendicular to T; distinctly expanded, rounded; upper margin markedly toothed, along its extent, numerous teeth (more than 10); not distally projected; back margin not folded.

Female holotype: (Figs. 85–87, 92, 93). All characters as in male except: Carapace 4.9 long; maximum width 3.85; minimum width 2.73. AME diameter 0.29; PLE 0.23; PME 0.2; PME less than $\frac{1}{4}$ PME diameter from PLE.

Chelicerae 2.38 long, about $\frac{2}{5}$ of carapace length in dorsal view; fang medium-sized, 1.47. Lengths of female described above: fe1 3.63; pa1 2.56; ti1 3.17; me1 3.08; ta1 0.7; total 13.14; fe2 3.4; pa2 2.42; ti2 3.12; me2 2.8; ta2 0.7; total 12.44; fe3 2.84; pa3 1.63; ti3 1.77; me3 2.66; ta3 0.74; total 9.64; fe4 3.77; pa4 2.1; ti4 2.8; me4 3.45; ta4 0.84; total 12.96; relative length 1–4–2–3; fe palp 2.23; pa palp 1.16; ti palp 0.93; ta palp 1.3; total 5.62. Spination: palp, leg1, leg2 spineless. Fe3d spineless; ti3d spines arranged in two bands: proximal 1.2.1; distal 1.0.1; ti3v spines ar-



Figures 88-93.—*Dysdera spinidorsum*, right male bulbus. 88, DD frontal; 89, DD external; 90, DD posterior; 91, P internal. 92-93, *Dysdera spinidorsum*, spinnerets. 92, Right ALS; 93, Right PLS.

ranged in two bands: proximal 1.0.0; distal 1.0.0; with two terminal spines. Fe4d spines in two rows: anterior 2; posterior 6; ti4d spines arranged in two bands: proximal 0.0.1; distal 0.0.1; ti4v spines arranged in two bands: proximal 1.0.1; distal 1.0.1; with two terminal spines. Abdomen 5.88 long; whitish; cylindrical. Abdominal dorsal hairs 0.37 long; thick, roughly straight, compressed, lanceolate; uniformly, thickly distributed. Vulva (Figs. 85-87) DA not distinguishable from VA; rectangular; DA twice as wide as long; DF wide in dorsal view. MF well-developed, completely

sclerotized, projected backwards, longer than DA lateral length. VA frontal region completely sclerotized; posterior region sclerotized at most anterior area; AVD absent. S attached to membranous VA; arms as long as DA, clearly curved; ends projected forwards; neck hardly visible. TB usual shape. ALS (Fig. 92) with PS; remaining piriform spigots more external than MS, arranged in two rows; 11 + 1 piriform gland spigots; PMS, PLS (Fig. 93) with 10-15 aciniform gland spigots.

Intraspecific variation.—Male cephalothorax ranges in length from 4.41-4.69, fe-

Table 5.—Intraspecific spination variability of *Dysdera spinidorsum*.

	Proximal	Medial-proximal	Medial-distal	Distal
Tibia 3 dorsal	1.1–2.1	0	0	1.0.1
Tibia 4 dorsal	0–1.0–1.1	0	0	0.0.1
Tibia 3 ventral	1.0.0–1	0	0	0–1.0.0
Tibia 4 ventral	1.0.0–1	0	0	0–1.0.0
	Number of rows		Number of spines	
Femur 3 dorsal		0		0
Femur 4 dorsal		2		1–2/4–8

male from 4.55–5.67. PLE-PME from $\frac{1}{3}$ PME diameter to $\frac{2}{3}$. Cheliceral granulations distally reduced in some females. Spination variability in Table 5.

Additional material examined.—**Fuerteventura:** *Antigua*: Montañas de Tegú, road Antigua-Betancuria; N slope, 18 February 1995, 2♂, (Arnedo, Ribera & Oromí, #2841 UL, 2842 (description) UB); 6♀, (Arnedo, Ribera & Oromí, #2843-45 UL, 2849, 4066 UB); 10 juv., (Arnedo, Ribera & Oromí, #2846-48 UL, 4059-65 UB). *Betancuria*: Betancuria, around village, 18 February 1995, 2♀, (Arnedo, Ribera & Oromí, #2851, 4067 UB). *La Oliva*: N. of La Oliva (175 m), 6 January 1990, 1 juv., (H. Enghoff & M. Báez, 2668 ZMK). *Puerto del Rosario*: La Matilla, near village, 20 February 1995, 2♀, (Arnedo, Ribera & Oromí, #2854, 4069); 1 juv., (Arnedo, Ribera & Oromí, #4070 UB). From Montaña Muda to La Matilla, 6 January 1990, 1 juv., (H. Enghoff & M. Báez, 2664 ZMK). *Tuineje*: Cuchillos de Jacomar, between Jacomar and Toneles Valley 19 February 1995, 2 juv., (Arnedo, Ribera & Oromí, #2852, 4068 UB).

Distribution.—Endemic species from central and northern Fuerteventura.

When the log-transformed number of *Dys-*

dera species in each Canarian island is plotted against the log-transformed island age, a clear linear relationship is observed (Fig. 94). However, the statistical regression obtained was very poor ($r^2 = 0.317$). When a 95% confidence interval was considered, two islands seemed to depart from the general trend: Tenerife had more species than expected while Lanzarote was poorer in species than expected. Removing both values did not result in a much better fit for the regression ($r^2 = 0.620$). Nevertheless, when the two eastern islands were removed from the analysis (Fig. 95), the relationship was markedly improved ($r^2 = 0.866$).

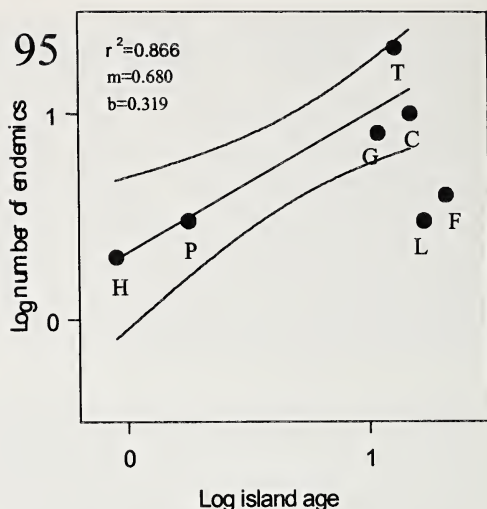
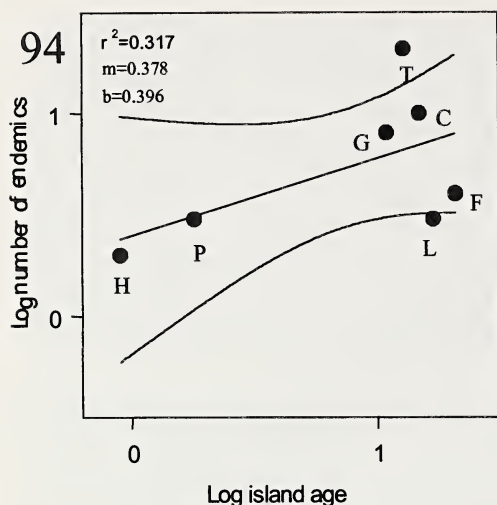
DISCUSSION

Morphological characters, and male genitalia in particular, suggest that with the exception of *D. lancerotensis*, the eastern endemic species are very closely related. Putative synapomorphies of this group include: the presence in the male bulb of a well-developed crest (C) along the internal margin of the anterior distal half region of the distal division, the presence of a lateral sheet apophysis and the presence of thick, lanceolate abdominal dorsal hairs. *D. sanborondon* only shares the first of these characters, which may indicate that it is basal. The presence of a flagellum in the male bulb, found in all but *D. alegranzaensis*, can also be found in some continental taxa, and is therefore likely to be a plesiomorphic state. Several characters support a sister-species relationship between *D. nesiotes* and *D. spinidorsum*: the enlargement of the internal margin of the anterior distal region of the distal division of the male bulb, and the posterior projection of the major fold (MF) lateral margins of the vulva.

Male bulb characters such as the presence

Table 6.—Number of endemics and the estimated age of each Canarian island. The values in brackets in the island age column are the ones used in the regressions.

Island	Num. of endemics	Island age (Mya)
Fuerteventura (F)	4	20–22 (21)
Lanzarote (L)	3	15–19 (17)
Gran Canaria (C)	10	14–16 (15)
Tenerife (T)	21	11.6–14 (13)
La Gomera (G)	8	10–12 (11)
La Palma (P)	3	1.6–2 (1.8)
El Hierro (H)	2	0.8–1 (0.9)



Figures 94, 95.—Regression plots of the log-transformed number of endemics against log-transformed island ages (upper and lower curves representing 95% confidence interval). 94, all the islands included in the regression; 95, Eastern islands excluded from the regression. (r^2 = regression coefficient, m = slope, b = constant). Abbreviations as in Table 6.

of the medial apophysis (MA), an arch-like ridge at the distal division anterior distal tip, and a free posterior apophysis, ally the eastern endemic *D. lancerotensis* to the “croco” group of species proposed by Deeleman-Reinhold & Deeleman (1988), which are distributed through southwestern Europe and northern Africa. Therefore, *D. lancerotensis* could be the result of an independent colonization event of the eastern islands.

A striking feature of Canarian *Dysdera* is that their distribution areas largely overlap (Arnedo et al. 1996; Arnedo & Ribera 1997). This pattern is also present in the eastern islands. In Fuerteventura, *D. spinidorsum* is found in the two known localities of *D. sanborondon*, while in Lanzarote and the northern islets *D. alegranzaensis* and *D. nesiotis* co-occurred in most of the collection localities. Although clear size segregation exists between *D. sanborondon* and *D. spinidorsum*, no morphological differentiation that would seem relevant to ecological differentiation is found between *D. alegranzaensis* and *D. nesiotis*. The species *D. longa* from Fuerteventura presents the only case of intra-island allopatric distribution, as it is restricted to the peninsula of Jandía. Several examples of allopatric distributions in arthropods and slugs between Jandía and the remaining regions of Fuerteventura have also been reported (Hut-

terer 1989; Juan et al. 1998). Finally, *D. lancerotensis* is spread throughout the eastern islands and is sympatric with all other eastern endemics.

While the sympatric distribution of *D. lancerotensis* may have secondarily resulted from an independent colonization, this does not seem to be the case for the remaining species. As described above, the eastern Canaries are part of a single volcanic ridge parallel to the African coast. The depths between the islands are small (less than 40 m between Fuerteventura, Lanzarote and the islets) and it is probable that all were connected several times during glaciation events. This would help to explain the presence of the same three *Dysdera* species inhabiting both Lanzarote and the northern islets. However, this geological scenario raises some questions regarding species distributions on the two main islands. Only one of the six eastern endemic species is shared between Lanzarote and Fuerteventura. This pattern could suggest several rounds of species exchange, with some recent enough to preclude morphological differentiation. *D. lancerotensis* provides an example. In contrast, the allopatric distribution of *D. nesiotis*-*D. spinidorsum* sister species pair suggests a more ancient vicariance event.

The presence of *D. nesiotis* in the Selvagens Islands is also unusual. Other examples

of shared species between Lanzarote-northern islets and the Selvagens are also known: the spiders *Oecobius lampeli* (Araneae, Oecobiidae) and *Ozyptila atlantica* (Araneae, Thomisidae) have been reported from the Selvagens and the eastern Canaries (Wunderlich 1991); the beetle *Macrocoma oromiana* (Coleoptera, Chrysomelidae) can be found both in Selvagens and Alegranza; the genus *Ifnidius* (Coleoptera, Malachiidae) includes one species from Ifni, one species from Lanzarote-Alegranza and one species from the Selvagens; and the Selvagens endemic *Cardiophorus oromii* (Coleoptera, Elateridae) has its closest relatives in the eastern Canaries. Although the origin of the Selvagens Islands traces back to the Oligocene, most of the present-day emergent lands is likely to be the result of quaternary volcanic activity after a long period of immersion under the ocean (Bravo & Coello 1978). Therefore, *D. nesiotis* probably colonized the Selvagens Islands from Lanzarote-northern islets in relatively recent times.

Surprisingly, none of the material studied here could be assigned to the cosmopolitan species *D. crocata*. This species is widely distributed in places disturbed by human activity not only in the remaining Canaries but throughout the world. The same result was found by Wunderlich (1991), who also considered the only known report of this species in the eastern islands (Schmidt 1975) to be doubtful. Competitive exclusion by the presence of the very closely related *D. lancerotensis* may explain the absence of *D. crocata* in these islands.

The species diversity of an oceanic island is the product of colonization and local diversification (Paulay 1994). The relative contribution of each process to the actual species number is heavily influenced by parameters like the island area, the distance from biota sources and the geological age. Plots of number of species, after a substantial improvement of taxonomic knowledge, against island age indicates that the eastern islands harbor a significant lower number of endemic *Dysdera* species than the rest of the Canaries. A major ecological differentiation exists between the eastern Canaries and both the central and western ones. In the Canaries, a zone of temperature inversion is formed at an altitude of roughly 1000 meters. This is the result of the joint effect of the humid and cool tradewinds

of the NE and the dry trade winds from the NW. An almost permanent cloud belt is formed in this zone. This cloud belt is the main water supply of the islands. Due to their greater age, the eastern islands have been strongly eroded and their mountains rarely reach altitudes above 800 m. This fact prevents these islands from capturing the clouds and the humid trade winds. Moreover, a very dry and dusty wind blows from the nearby Sahara desert. This climatic regime brings about a lower diversity of habitats in the eastern islands compared to the central and western Canaries. The low number of endemics in the eastern islands could therefore be explained by extinction mainly related to the major environmental change that took place on these islands. The distribution of the eastern endemic specimens seems to support this hypothesis. Most of the specimens were collected from sites located on the northern slopes of massifs over 400 m high. These places represent the wettest parts of these islands. The single specimen (belonging to *D. nesiotis*) found in a dry habitat (the sand dunes of Malpaís de Corona) was captured by night. Nevertheless, *Dysdera lancerotensis* constitutes an exception to the rule. This species is spread over most of the island habitats, from mountain summits to lava fields, including places disturbed by human activity. An extremely high level of tolerance to a wide range of environmental conditions has already been reported for a closely related species, *D. crocata* (Cooke 1968).

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NEW SPECIES AND RECORDS OF *KLEPTOCHTHONIUS* FROM INDIANA (PSEUDOSCORPIONIDA, CHTHONIIDAE)

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ABSTRACT. New records and supplemental data are given for the troglobitic species *Kleptochthonius packardi*; and two new epigean or troglomorphic species are described, *K. griseomanus* and *K. lewisorum*. Some comments are made on the status of the genus.

Keywords: Pseudoscorpionida, *Kleptochthonius*, cavernicoles, Indiana

In 1879, H. Hagen described *Blothrus packardi* from Wyandotte Cave in Crawford County, Indiana. This was the first cavernicolous pseudoscorpion known in North America. Re-study of the type collection (Muchmore 1963) revealed that the species belongs in the genus *Kleptochthonius* Chamberlin 1949. In 1994 I reported an isolated *Kleptochthonius* palp from Wilson's Cave in Jefferson County, Indiana. No other material pertaining to the genus has been reported from the state until recently. Over the past several years, intensive search by J.J. Lewis and his colleagues in caves of southern Indiana has turned up new material of *K. packardi*, together with several other species of pseudoscorpions. The present paper reexamines *Kleptochthonius packardi* and describes two new species in the genus.

METHODS

Most of the specimens studied here were dissected, cleared, and mounted on microscope slides for detailed examination. Specimens are deposited in the Florida State Collection of Arthropods, Gainesville, Florida (FSCA) and the Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts (MCZ). Some abbreviations are used in the text: L = length; L/B = ratio, length/breadth; L/D = ratio, length/depth; T = tactile seta.

SYSTEMATICS

Genus *Kleptochthonius* Chamberlin

Apochthonius (*Heterochthonius*) Chamberlin 1929: 153; Beier 1932:42.

Heterochthonius Chamberlin: Hoff 1945:313; Hoff 1949:434.

Kleptochthonius Chamberlin 1949:4; Hoff 1958:7; Malcolm & Chamberlin 1961:2–3; Muchmore 1965:1; Muchmore 1990:510; Harvey 1991:177; Muchmore 1994a:13.

Chamberlinochthonius Vachon 1952:105; Hoff 1958:7.

Kleptochthonius (*Chamberlinochthonius*) Vachon: Malcolm & Chamberlin 1961:16; Muchmore 1965:1; Muchmore 1990:510; Harvey 1991:179.

Kleptochthonius was described originally by J.C. Chamberlin (1929) as *Heterochthonius*, a subgenus of *Apochthonius* Chamberlin. The name *Kleptochthonius* was first applied by Chamberlin (1949), after he discovered that the name *Heterochthonius* had been used previously by Berlese (1910) for a genus of Acarina. At that time, only two species were known, *K. crosbyi* (Chamberlin 1929) and *K. multispinosus* (Hoff 1945), both epigean forms from North Carolina. In 1952, M. Vachon erected a new, allied genus, *Chamberlinochthonius*, the type species, *C. henroti*, being a troglobitic form from a cave in West Virginia. Malcolm & Chamberlin (1961) described two new epigean species of *Kleptochthonius* from Oregon and eight new troglomorphic species from caves in eastern states; the latter they placed in *Chamberlinochthonius*, which they regarded as an “artificial but convenient” subgenus of *Kleptochthonius*. Subsequently, Muchmore (1963, 1965, 1976, 1994a, 1994b) and other authors (e.g., Harvey 1991) followed Malcolm & Chamberlin in assigning species to the subgenera *Kleptochthonius* or *Chamberlinochthonius*. However, subgeneric designations are not used in the present report, because they are currently undergoing reevaluation (see Discussion).

The genus *Kleptochthonius* was well defined by Malcolm & Chamberlin (1961). Supplementary discussions of specialized sensory setae on the palpal chela and of the dorsal process of the movable chelal finger were given by Muchmore (1965, 1976, 1994a).

Kleptochthonius packardii (Hagen)

Figs. 1, 4

Blothrus packardii Hagen 1879:399.

Chthonius packardii (Hagen): Hagen 1880:83–84; Hubbard 1880:37, 79, 84 (in part); Banks 1895:13 (in part); Blatchley 1897:170; Coolidge 1908:114 (in part); Vachon 1952:111 (in part).

Chthonius packardii Hagen: Packard 1888:43–48, figs. 12a–g, Pl. XI figs. 3, 3a–j (in part).

Chthonius [sic] *packardii* Hagen: Blatchley 1897:205 (in part).

Chthonius [sic] *packardii* Hagen: Blatchley 1897:171.

Chthonius(?) *packardii* (Hagen): Beier 1932:61 (in part); Roewer 1937:240 (in part); Hoff 1958:4 (in part).

Genus? *packardii* Hagen: Hoff 1949:443 (in part).

"*Chthonius*" *packardii* (Hagen): Malcolm & Chamberlin 1961:1.

Kleptochthonius (*Chamberlinochthonius*) *packardii* (Hagen): Muchmore 1963:2–5, figs. 1–2; Muchmore 1965:2, 7; Muchmore 1976:211; Harvey 1991:181 (in part); Muchmore 1994b:319–320.

Not *Chthonius packardii* Hagen [sic]: Giovannoli 1933:604 (misidentification).

Type material examined.—Lectotype male (No. 1), allotype female (No. 2), and 4 paralectotype males of *Blothrus packardii* Hagen [also labeled "*Chamberlinochthonius packardii* (Hagen), det. W.B. Muchmore"], on slides, in MCZ.

Type locality.—Wyandotte Cave, Crawford County, Indiana. [Note: Harvey (1991:181) erroneously gives "Mammoth Cave, Kentucky, U.S.A." as the type locality of *K.(C.) packardii*.]

Diagnosis.—A large, eyeless species of *Kleptochthonius* with very slender appendages (length of palpal chela 1.3 mm or greater, chela usually 7.0 or more times as long as broad); all parts light brown or lighter; dorsal process on proximal end of movable chelal finger long, cylindrical; a short, stout sensory seta on medial side of fixed finger near base.

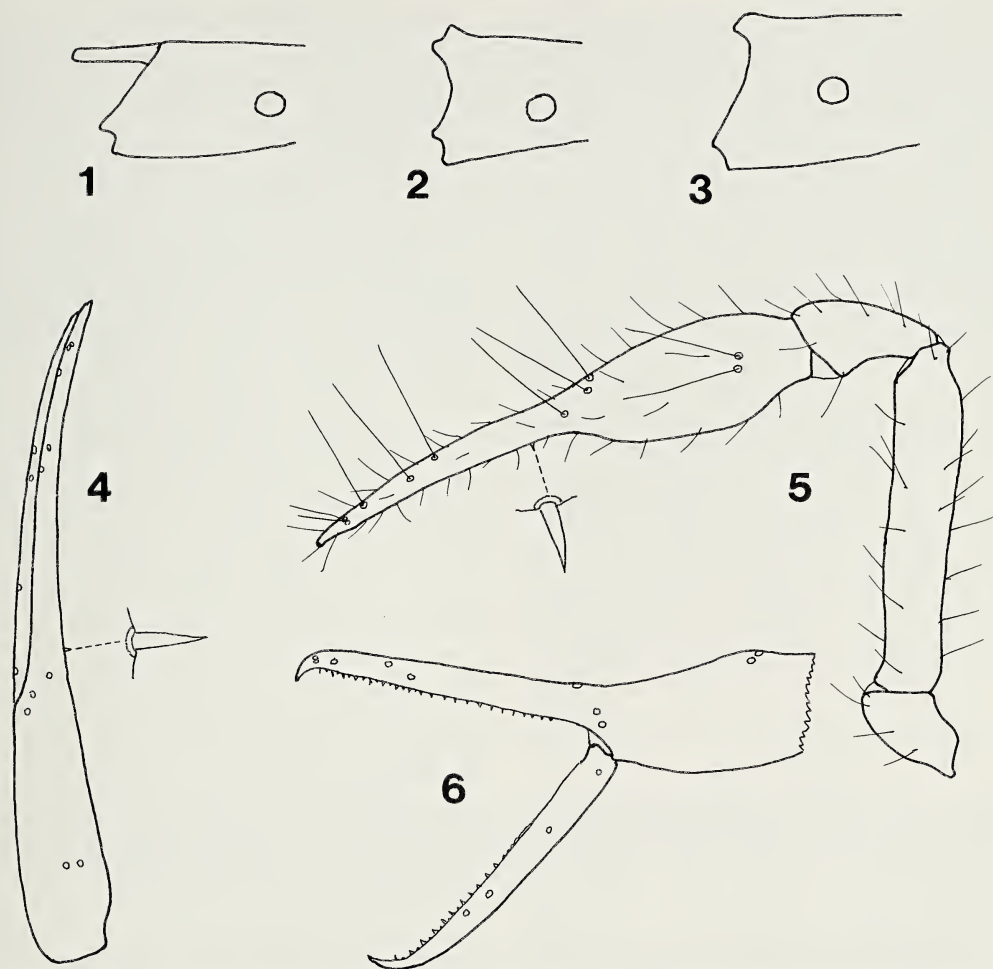
Additional material examined.—INDIANA: *Crawford County*: Route 66 Cave, 6 km S of Hardinsburg, "hand-collected from raccoon scat (with *Collembola*) on mudbank, end of main passage of cave about 60 meters from entrance, dry upper level", 26 October 1996 (J.J. Lewis, James Lewis, V.

Lewis), 1♀. *Harrison County*: Binkley Cave, about 1.5 km S of Corydon, in pitfall trap about 300 m into dark zone, 16 November 1997 (J.J. Lewis, T. Sollman), 1 tritonymph; Coon Cave, 6.5 km SW of Corydon, "from rock on top of baited (cheese) pitfall trap, dark zone", 17 May 1997 (J.J. Lewis, S. Rafail), 1♂; Maucks Cave, Harrison-Crawford State Forest, "from flowstone in lower level of cave", 14 September 1996 (J.J. Lewis, James Lewis, V. Lewis), 1 tritonymph; Twin Domes Cave, Twin Domes Nature Preserve, in pitfall traps, 31 May 1998 (J.J. Lewis), 2♀. *Orange County*: Murray Spring Cave, Paoli Country Club, in pitfall trap, 30 April 1998 (J.J. Lewis, S. Rafail), 1♀; Saltpeter Cave, 6 km NNE of Marengo, 2 March 1997 (J.J. Lewis, James Lewis, V. Lewis), 2♀. (All on slides, in FSCA.)

Supplemental data.—All parts of animals pale in color. Eyes absent in all. Chaetotaxy of carapace 4-4-4-2-4 = 18, except in one female where there are 3, rather than 4, setae on posterior margin. Tergal chaetotaxy somewhat variable, but usually much like the types, i.e., 2-3:2-3:2-3:2-4:4:4:5-6:6:-. Internal genitalia of male similar to those of *K. crosbyi* (see Malcolm & Chamberlin 1961: fig. 3A). Appendages of adults very long and slender. Palpal femur 1.55–1.65× and chela 2.3–2.45× as long as carapace; L/B of femur 6.85–7.15, patella 2.35–2.55, chela 7.1–7.9; L/D of hand 2.75–3.05; movable finger 1.55–1.7× as long as hand. Leg I: femur 2.25–2.5× as long as patella. Leg IV: L/D of femur + patella 3.45–3.85, tibia 5.25–5.7. The dorsal process on the proximal end of movable finger of chela is long, cylindrical (Fig. 1). There is a short sensory seta on the medial side of the fixed finger of the palpal chela, at or just distad of level of trichobothrium *ist* (Fig. 4).

Tritonymph much like adult but smaller and with slightly less slender appendages; with only 7 trichobothria on hand and fixed chelal finger and 3 on movable finger. Short sensory seta on fixed chelal finger as in adult.

Measurements (mm).—*Adult*: Figures given first for the single male, followed in parentheses by ranges for 6 females. Body L 1.90 (1.81–2.63). Carapace L 0.605 (0.59–0.695). Chelicera L 0.53 (0.51–0.57). Palp: trochanter 0.30 (0.28–0.32) / 0.155 (0.13–0.17); femur 1.00 (0.97–1.11) / 0.14 (0.14–0.155); patella 0.36 (0.355–0.39) / 0.15 (0.15–0.16); chela 1.50 (1.42–1.60) / 0.19 (0.19–0.22); hand 0.60 (0.55–0.63) / 0.195 (0.19–0.22); movable finger L 0.94 (0.89–1.04). Leg



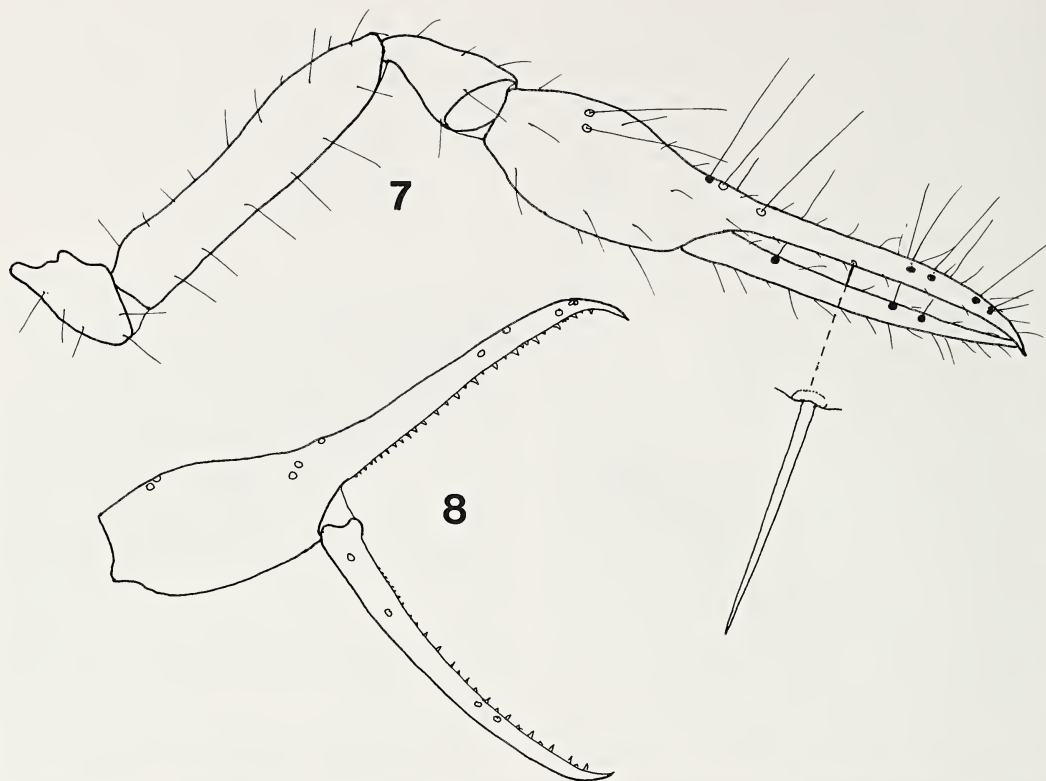
Figures 1-6.—Species of *Kleptochthonius*. 1-3. Proximal end of movable finger of palpal chela, lateral view, showing dorsal process (dorsal at top; areole is that of trichobothrium *b*). 1. *Kleptochthonius packardii*, lectotype male; 2. *Kleptochthonius griseomanus* new species, holotype female; 3. *Kleptochthonius lewisorum* new species, holotype female. 4. *Kleptochthonius packardii*, lectotype male: Left palpal chela, dorsal view, with enlargement of sensory seta on fixed finger (other setae omitted). 5, 6. *Kleptochthonius griseomanus* new species, holotype female. 5. Right palp, dorsal view, with enlargement of sensory seta on fixed finger; 6. Left chela, lateral view (base broken; setae omitted).

I: femur 0.62 (0.585-0.665) / 0.095 (0.08-0.11); patella 0.265 (0.235-0.295) / 0.09 (0.08-0.09). Leg IV: femur + patella 0.865 (0.86-0.955) / 0.245 (0.23-0.26); tibia 0.60 (0.555-0.63) / 0.105 (0.105-0.12).

Tritonymph: Two specimens. Body L 1.45, 1.68. Carapace L 0.49, 0.495. Chelicera L 0.40, 0.40. Palp: femur 0.75, 0.76 / 0.125, 0.125; patella 0.28, 0.29 / 0.125, 0.13; chela 1.13, 1.14 / 0.17, 0.17; hand 0.46, 0.45 / 0.17, 0.17; movable finger L 0.69, 0.71. Leg IV: femur + patella 0.605, 0.64 / 0.16, 0.18; tibia 0.42, 0.45 / 0.09, 0.09.

Remarks.—The newly collected specimens appear to be slightly larger than the types from Wyandotte Cave, as reported in 1963. However, these differences are probably due in part to changes in measuring techniques between that time and the present. In any event, the species, as here recognized, is rather variable in size and chaetotaxy. Further collecting and study may reveal that more than one species is represented.

In addition to the type locality, Wyandotte Cave, *Kleptochthonius packardii* has been found in several caves in neighboring Craw-



Figures 7, 8.—*Kleptochthonius lewisorum* new species, holotype female. 7. Left palp, dorsal view but chela twisted showing medial surface, with enlargement of sensory seta on fixed finger (darkened areoles are underneath, i.e., on lateral side of chela); 8. Right chela, lateral view (setae omitted).

ford, Harrison, and Orange Counties, Indiana. Two females were collected within Twin Domes Cave, Harrison County, where *K. grieseomanus* new species is also present at the entrance. A tritonymph, apparently belonging to *K. packardi*, was taken some 300 m into the eastern end of the Binkley Cave System, the largest known cave in Indiana, while the holotype of *K. lewisorum* new species (see below) was found in the Baelz Cave section at the western end of the system (about 5.5 km away, straight-line distance) (see Lewis & Sollman 1998).

Kleptochthonius(?) sp.

A single, detached, left palp of an adult pseudoscorpion was collected in Wilsons Cave, Jefferson County, Indiana; it has been tentatively identified as belonging to an unknown species of *Kleptochthonius* (Muchmore 1994b). If it is indeed a *Kleptochthonius*, it appears most closely related to *K. sheari* Muchmore (1994a), with a relatively long,

sensory seta at the base of the fixed chelal finger. From the attenuation of the palp, it appears to be a troglomorphic species. No other representative of the genus has been found in this part of Indiana.

Kleptochthonius grieseomanus new species
Figs. 2, 5, 6

Type material.—Holotype female (WM8208.01001) from Indian Cave, (a sandstone cave in the Hemlock Cliffs area of Hoosier National Forest), about 6.5 km SSE of Taswell, Crawford County, Indiana, 5 July 1997 (J.J. Lewis, S. Rafail); allotype male (WM8240.02001) from leaf litter at base of entrance pit, Twin Domes Cave, Twin Domes Nature Preserve, Harrison County, Indiana, 31 May 1998 (J.J. Lewis, R. Burns, E. Burns, H. Huffman, E. Jacquart) (mounted on slides, in FSCA).

Diagnosis.—A smaller, less slender species, with palpal chela 1.05 mm long, 4.7–5.05× as long as broad; 4 corneate eyes;

mostly light brown, but hand of chela distinctly gray; dorsal process on proximal end of movable chelal finger small, roughly bilobed; a short, stout sensory seta on medial side of fixed finger near base. *Kleptochthonius griseomanus* appears most closely related to *K. inusitatus* Muchmore (1994a) from eastern Ohio. The two are similar in size and proportions, but *K. griseomanus* differs in having a distinctly gray palpal chela, fewer setae on the terga, a smaller, less strongly bilobed process on the base of the movable finger of the chela, and the small sensory seta on the fixed finger closer to the level of trichobothrium *ist*.

Description.—Representative of *Kleptochthonius* as discussed above, and with the following particular features. Male and female much alike. Hand of palpal chela gray; chelal fingers and other palpal segments, carapace and chelicera tan; other parts lighter. Carapace about as long as broad; epistome barely perceptible; 4 corneate eyes; chaetotaxy 6-4-4-2-4 = 20. Coxal area typical; each coxa I with 5 coxal spines. Tergal chaetotaxy of holotype 4:4:7:6:8:9:10:9:?:?:T2T:0, allotype similar. Sternal chaetotaxy of holotype (female) 8: (3)8(3):(3)8(3):12:14:14:13:13:11:0:2; sternites 2–5 of male 13:11-10 / (3)6(3):(3)9(3): 11. Internal genitalia of male similar to those of *K. crosbyi* (see Malcolm & Chamberlin 1961: fig. 3A). Chelicera 0.8 as long as carapace; hand with 7 setae; flagellum of about 7 setae; galea a very low elevation. Palp (Fig. 5) long and slender; femur 1.3–1.35 \times and chela 1.9–1.95 \times as long as carapace. L/B of trochanter 1.8–1.85, femur 5.5–5.85, patella 2.1–2.15, and chela 4.7–5.05; L/D of hand 1.95–2.05; movable finger 1.5 \times as long as hand. Trichobothria as shown in Fig. 6. A short, sensory seta is present distad of trichobothrium *ist* on medial side of fixed finger (Fig. 5). Dorsal process on base of movable finger small, roughly bilobed (Fig. 2). Fixed finger of holotype with 21 tall, spaced macrodenticles and 10 very small, rounded microdenticles alternating distally; movable finger with 11 tall, spaced macrodenticles, 6 very small alternating microdenticles, and 10 low, rounded teeth proximally. Legs rather long and slender. Leg I with femur 2.1–2.2 \times as long as patella. Leg IV: L/D of femur + patella 2.9–3.0, tibia 4.9–5.1.

Measurements (mm).—Figures given first for holotype female, followed in parentheses

by those for allotype male. Body L 2.11 (1.87). Carapace L 0.555 (0.54). Chelicera L 0.45 (0.42). Palp: trochanter 0.235 (0.23) / 0.13 (0.125); femur 0.725 (0.73) / 0.13 (0.125); patella 0.32 (0.295) / 0.15 (0.14); chela 1.04 (1.06) / 0.22 (0.21); hand 0.43 (0.435) / 0.22 (0.21); movable finger L 0.64 (0.66). Leg I: femur 0.39 (0.415) / 0.075 (0.075); patella 0.185 (0.185) / 0.075 (0.075). Leg IV: femur + patella 0.615 (0.66) / 0.20 (0.23); tibia 0.435 (0.46) / 0.09 (0.09); basitarsus 0.245 (0.235) / 0.075 (0.065); telotarsus 0.415 (0.445) / 0.05 (0.05).

Etymology.—The species is named *griseomanus* in reference to the distinctly gray hand of the palpal chela.

Remarks.—Two specimens of *K. packardi* were collected within Twin Domes Cave, in the entrance pit of which the allotype of *K. griseomanus* was found (see above). The former is certainly a troglobite, whereas the latter is at best a troglophile, or an epigeal species only accidentally associated with the cave.

Kleptochthonius lewisorum new species

Figs. 3, 7, 8

Type material.—Holotype female (WM8207.01001) from the “underside of a stone lying in leaf litter with some raccoon droppings, in the company of some troglobitic *Sinella alata* Christiansen (Collembola), twilight zone,” Baelz Cave, Binkley Cave System, Harrison County, Indiana, 28 June 1997 (J.J. Lewis, F.A. Pursell) (mounted on slide, in FSCA).

Diagnosis.—A medium-sized species (palpal chela 1.15 mm long), with moderately slender palps (chela 4.6 \times as long as broad); 4 eyes, posterior pair smaller than anterior pair; all parts, including palps, light brown or lighter; process on proximal end of movable finger of palpal chela small, irregularly rounded; a moderately long sensory seta on medial side of fixed finger near middle.

Description of female.—(Male unknown). Representative of the genus *Kleptochthonius* as discussed above, and with the following particular features. Palps very light brown, carapace and chelicerae tan, other parts lighter. Carapace with epistome very small; 4 corneate eyes, posterior pair smaller; chaetotaxy 9-4-4-2-4 = 23. Coxal area typical of the genus; each coxa I with 3 coxal spines. Tergal chaetotaxy 4:4:4:6:7:9:9:9:9:7:T2T:0.; sternal

chaetotaxy 8:(4)6(4):—?—T1T2T1T:2. Chelicera 0.75 as long as carapace; hand with 7 setae; flagellum of 7–8 setae; galea a low elevation. Palp (Fig. 7) long, slender: femur $1.3\times$ and chela $1.95\times$ as long as carapace. L/B of trochanter 1.9, femur 5.05, patella 1.75, and chela 4.6; L/D of hand 1.6; movable finger $1.85\times$ as long as hand. Trichobothria as shown in Fig. 8. A sensory seta of moderate length on fixed finger near middle of medial side (Fig. 7). Dorsal process on base of movable finger small, irregularly rounded (Fig. 3). Fixed finger with about 20 tall, spaced macrodenticles, decreasing in size to very small proximally, and 10 moderately large microdenticles alternating distally (in two of the intervals between macrodenticles there are two microdenticles rather than one); movable finger with 10 tall, spaced macrodenticles, 6 moderately large alternating microdenticles, and 10 low, rounded teeth proximally. Legs moderately slender: leg I with femur $2.1\times$ as long as patella; leg IV with L/D of femur + patella 2.95, of tibia 4.5.

Measurements (mm).—Body L 2.47. Carapace L 0.54. Chelicera L 0.445. Palp: trochanter 0.265/0.14; femur 0.755/0.15; patella 0.295/0.17; chela 1.15/0.25; hand 0.42/0.265; movable finger L 0.78. Leg I: femur 0.39/0.08; patella 0.185/0.08. Leg IV: femur + patella 0.615/0.21; tibia 0.43/0.095; basitarsus 0.235/0.08; telotarsus 0.43/0.045.

Etymology.—The species is named for Julian J. Lewis and his sons, James J. Lewis and Victor M. Lewis, who for the past several years have been leading the way in studies of the invertebrate faunas in Indiana caves.

Remarks.—Because of the moderately long sensory seta near the middle of the fixed chelal finger, *Kleptochthonius lewisorum* appears related to one or more, as yet unidentified, species from the southeastern states. It differs from them in size, proportions, and body chaetotaxy.

Baelz Cave, the type locality, consists of a short passage in the bluff of Indian Creek near the Seven Springs resurgence of Binkley River; it is a route for floodwater overflow out of the Binkley Cave System. This is about 6 km from the site of capture of a specimen of *K. packardi* in the eastern end of the system (see above).

DISCUSSION

Like *Tyrannochthonius* Chamberlin 1929 (see Muchmore & Chamberlin 1995; Muchmore 1996) the genus *Kleptochthonius* contains species with quite varied morphologies. On the one hand, *Kleptochthonius crosbyi* (type species of the genus) is a small, four-eyed, epigean chthoniid, with moderately slender palps, while *K. henroti* (Vachon) (type species of *Chamberlinochthonius* Vachon) is a large, blind, troglobitic species with very attenuated palps. In their revision of *Kleptochthonius*, Malcolm & Chamberlin (1961) recognized the close relationship of these varied species by “considering *Chamberlinochthonius* Vachon as an artificial but convenient subgenus comprising essentially the cavernicolously modified forms of *Kleptochthonius*.” (p. 3). Now, when there are some 10 epigean species and over 30 cavernicolous species known in the genus, it is perfectly clear that a generic or subgeneric distinction based on size, eyes, coloration, or slenderness of appendages is not warranted. However, it does appear possible that the nature and number of special sensory setae on the fixed finger of the palpal chela (Muchmore 1976, 1994a), and perhaps some other characters (Muchmore 1965), will provide evidence of separate evolutionary lines within the genus. Restudy of all species in the genus is in progress.

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SPIDER SIZE AND LOCOMOTION ON THE WATER SURFACE (ARANEAE, PISAURIDAE)

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ABSTRACT. Newly emerged fishing spiders, *Dolomedes triton* (Walckenaer 1837), can achieve rowing velocities as high as those of adults despite an approximately 600-fold difference in mass (1.7 mg vs. 1.1 g). In contrast, when velocity is measured in relative terms (body lengths/sec), small spiders move much more rapidly than adults, with $V_{rel} \propto \text{mass}^{-0.31}$. This surprising performance of very small spiders can be attributed both to their very high stride frequency ($f_s \propto \text{mass}^{-0.43}$) and to the high angular velocity of their propulsive legs ($\omega \propto \text{mass}^{-0.33}$). Calculations of leg tip velocities, based on measurements of both angular velocities and leg lengths, reveal that maximum leg tip velocities are achieved by spiders of about 33 mg, nineteen times more massive than the smallest spiders we tested. Some very small spiders perform conspicuously and consistently less well than do others of the same size. A detailed dissection of the motion of these underachievers reveals that a disproportionate amount of their rowing effort goes into vertical as opposed to horizontal work: the ratio of vertical to horizontal work during rowing is $1.03 \pm 0.89 : 1$ in normal fishing spiders and $5.18 \pm 1.73 : 1$ in the underachievers.

Keywords: Allometry, locomotion, size, spider, aquatic

Locomotion across the surface of water is performed both by fishing spiders (Arachnida, Araneae, Pisauridae) (McAlister 1959; Shultz 1987) and by water striders (Insecta, Hemiptera, Gerridae) (Anderson 1976). This form of locomotion involves not only support by the water's surface tension but also drag resistance to leg motion as the animals push backward to propel themselves forward. Crucial for the rowing gait in this semi-aquatic locomotion is the dimple formed in the water surface as the animal's leg pushes first down and then backward, because it is the leg with its dimple that encounters resistance as it moves horizontally, and it is that resistance against which the animal pushes to achieve forward acceleration (Suter et al. 1997). When the leg pushes too deeply into the water or moves horizontally too rapidly, the dimple disintegrates, leaving the leg alone, without the dimple, to provide forward thrust. The leg without the dimple encounters far less drag resistance because its effective frontal surface area is much smaller (Suter & Wildman 1999).

This unorthodox form of locomotion, available only to relatively small creatures, is performed by pisaurid spiders of all ages and consequently of all sizes. In one of the most common pisaurids in North America, *Dolomedes triton* (Walckenaer 1837), adult females

at about 1 g are approximately 600 times as massive as hatchlings, a difference that should, in theory, result in substantial differences in the efficacy of rowing locomotion. Is there a relatively simple allometric relationship between size and rowing efficacy in pisaurid spiders?

The allometric properties of aerial, terrestrial, and submerged locomotion have been studied in considerable detail (for references, see Pennycuik 1992; Calder 1984; Peters 1983). The allometry of locomotion on the water surface, however, has received very little attention: both Vogel (1994) and Denny (1993) have speculated about the difficulties that may be faced by very small organisms (e.g., juvenile water striders) attempting to push against a very slippery water surface, and we have published some data on allometric relationships (Suter et al. 1997; Suter & Wildman 1999) in support of specific arguments about the biomechanics of rowing in fishing spiders. Heretofore, there has been no explicit investigation of the relative efficacy of rowing locomotion for very small vs. much larger arthropods. Thus, the primary reason for undertaking the empirical studies on which we report here is the need to fill that gap in our knowledge. The secondary reason for these studies is derived from the observation

(Suter unpubl. obs.) that very young fishing spiders in the genus *Dolomedes* hunt primarily in terrestrial and emergent vegetation whereas adolescents and adults hunt more frequently at the water surface. The current study, if it demonstrates substantial size-specific differences in rowing efficiency, could help to explain the motivation for changing foraging behavior during maturation.

METHODS

Organisms.—The species of fishing spider used in this study, *Dolomedes triton* (Araneae, Pisauridae), can become quite large (adult females: to 1.5 g, 2 cm body length, and 9 cm leg span), and normally inhabit marshes and the edges of ponds and streams throughout much of North America (Gertsch 1979). The larger subjects (> 0.1 g) for these experiments were collected from small ponds in Mississippi and held in our laboratory (maintenance and experimentation at 22–25 °C) in 3.8 liter plastic aquaria containing water (about 2 cm deep) and an inverted clay flower pot to provide a solid substrate. We fed these spiders assorted insects and changed their water approximately once a week. The smaller subjects (1.7–100 mg) were hatched in the laboratory from an egg case borne by an adult female captured (as above) in Mississippi. The locomotion of the smallest subjects (1.7 mg) was studied while they were still 2nd instar hatchlings and had not yet eaten. These and the other small spiders were first reared communally in a 19 liter aquarium containing 2 cm of water and several rocks to furnish solid substrate (although they seldom left the glass walls of the aquarium), and were provided with live fruit flies (*Drosophila melanogaster* and *D. virilis*) and each other *ad lib*.

The largest of the adult fishing spiders (1.05 g) was 610 \times as large as the smallest of the hatchling spiders (1.72 mg), providing us with more than 2.5 orders of magnitude in mass variation against which to scale the several parameters of surface locomotion.

High-speed videography.—Because most of the motion involved in the spiders' rowing movements across the surface of water occurs in the horizontal plane, we videotaped their locomotion from directly above. The arena used in videotaping the locomotion of all but the smallest spiders consisted of a white porcelain-surfaced tray, a smooth, circular plastic

barrier to prevent the spider's escape, and a layer of water at least twice as deep as the deepest dimple we had observed for a spider of the size of the test spider. We used the bottom section of a small petri dish (6.0 cm diameter) as the arena for videotaping the locomotion of the smallest spiders. The arenas were lit with an incandescent point source (subtending an angle of 0.28° when 60 cm from the spider), mounted at 45° above and to one side of the videotaped part of the arena. We adjusted the camera's aperture to obtain sufficient depth of field to allow both the spider and its shadow (on the porcelain surface of the arena or on a white sheet of paper under the petri dish) to be in sharp focus.

During a trial, we placed a test spider in the arena, recorded its movements at 1000 fps with a Kodak EktaPro EM-1000 video recorder, and stored the images in S-VHS format. We analyzed the spider's motion in the horizontal plane by using Image (NIH shareware) to digitize and record the coordinates of the anterior and posterior tips of the body and the angles of legs III and II (relative to the body's long axis) either every 1 ms (for small spiders) or every 5 ms. We used the body coordinates to measure the spider's length, to analyze the displacement of the spider through time in both absolute and relative terms, and to calculate the pitch (p , degrees) of the body [$p = \cos^{-1}$ (apparent length/true length)] as it changed during the rowing stride cycles. We used changes in leg angles over time to estimate the angular velocity of the leg and the velocity of its tip during the power phase of rowing locomotion.

To estimate the horizontal component of the force exerted by a spider during a rowing stroke, we graphed the spider's velocity (m/s) as a function of time (s) and used the slope of the linear part of the line as our estimate of acceleration (Suter et al. 1997). We then applied Newton's second law ($F = ma$) to calculate the average net force exerted by the spider during acceleration in the horizontal plane.

To estimate the horizontal work done during a rowing stroke, we multiplied the horizontal component of force by the distance the spider traveled during the application of the force ($w = mad$). To estimate the vertical work done during a rowing stroke, we used the measurements of pitch to calculate the maximum change in the height of the spider's

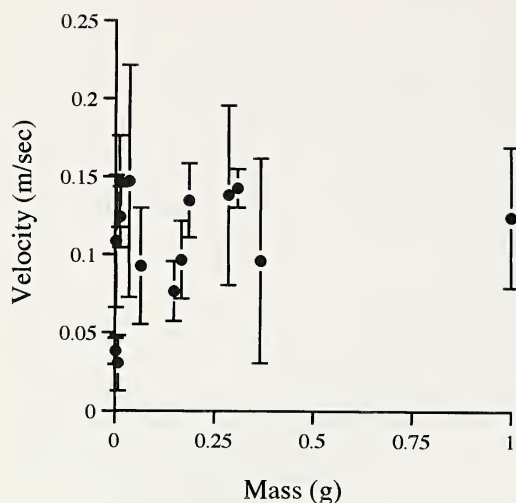


Figure 1.—The relationship between *Dolomedes triton* mass and velocity (mean \pm SD). Especially for very small spiders, between-individual variance is high; standard deviations indicate substantial variability within individuals.

center of mass (Fig. 9). That change in height required work against gravity ($w = mgh$).

RESULTS

Actual horizontal velocities achieved by spiders rowing across the surface of distilled water averaged 0.107 ± 0.038 m/sec (mean \pm SD of the means of 14 individuals, 51 trials total) and showed no obvious systematic changes with spider mass (Fig. 1). Within-individual variation was high for some spiders, likely a consequence of differences in effort as reflected in differences in the angular velocities of the propulsive legs (Suter et al. 1997; Suter & Wildman 1999). When the logarithms of velocities were plotted against the logs of spider masses, however, it became clear that inter-individual differences were substantially greater for very small spiders than for larger ones (Fig. 2). Two individuals, both with average velocities < 0.05 m/sec, were outliers in a population of spiders whose average velocities otherwise remained between 0.08 m/sec and 0.15 m/sec. Because the outliers had masses < 0.03 g, we included in our analysis a treatment of two groups that were defined by spider size (the five spiders with masses < 0.03 g, two of which were the outliers, and the nine larger spiders).

Although absolute rowing velocities did not

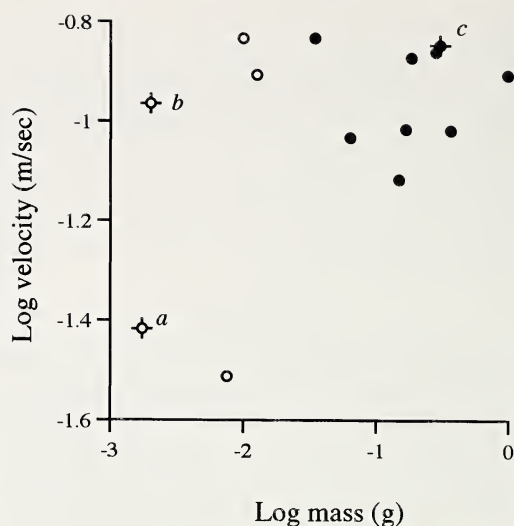


Figure 2.—The log-log relationship between spider mass and velocity. Spiders greater than 0.03 g (●) had mean rowing velocities > -1.2 log m/s whereas spiders with masses less than 0.03 g (○) had a bimodal distribution of mean rowing velocities with three individuals attaining velocities comparable to those of the larger spiders and two individuals having mean velocities < -1.4 log m/s. To elucidate the differences among the large and the two modes of small spiders, the rowing locomotion of three spiders (indicated by “+”; a, 1.7 mg; b, 2.0 mg; c, 308 mg) is characterized in detail in Figure 5 and is highlighted in Figures 3, 4, and 10).

vary systematically with mass, relative velocities, V_{rel} (body lengths/sec), decreased substantially and significantly with increasing mass (Fig. 3). The relationship for only the larger spiders (> 0.03 g) was $V_{rel} = m^{-0.32}$ ($r^2 = 0.653$, $n = 9$, $P < 0.01$) and that relationship changed only slightly when the smaller spiders were included in the analysis ($V_{rel} = m^{-0.31}$; $r^2 = 0.785$, $n = 14$, $P < 0.01$). This strong relationship may be a consequence, in part, of the fact that stride frequency, f_s (strides/sec), also decreased significantly with increasing mass (Fig. 4; for larger spiders, $f_s = m^{-0.36}$ and for all spiders, $f_s = m^{-0.43}$).

In an effort to understand the causes of the quantitatively very different performances of individuals of the same small mass and the very similar performances of individuals of divergent masses, we analyzed in detail the locomotor behavior of three spiders (*a-c* in Figs. 1–3). In this trio, *a*, *b*, and *c* had masses

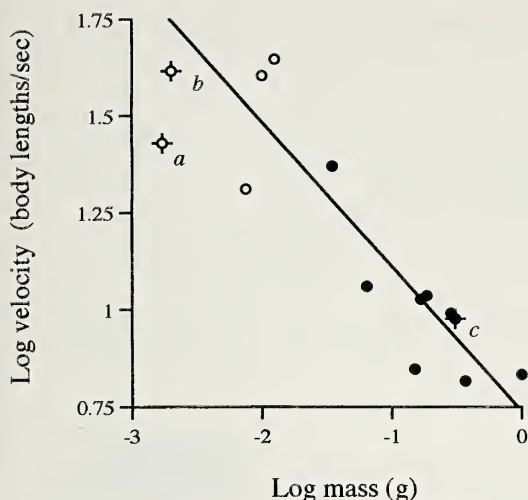


Figure 3.—The log-log relationship between spider mass and relative velocity measured in body lengths traveled per second. A linear fit to all points indicates $\text{Log}_{10}V = -0.305 \text{ Log}_{10}m$ ($n = 13$, $r^2 = 0.785$, $P < 0.01$). When we removed spiders smaller than 0.03 g from the analysis, the slope of the linear fit changed only slightly, to -0.320 ($n = 9$, $r^2 = 0.653$, $P < 0.01$).

of 1.7, 2.0, and 308 mg respectively, but had mean absolute velocities of 0.038, 0.109, and 0.143 m/sec respectively. The spiders' horizontal velocities varied over time, rising linearly during the propulsive phase of each stride and decreasing during the recovery phase (Fig. 5, top row). The acceleration was, in each case, accompanied by a rapid rise in the area of the shadows cast by the dimples made by legs III and II (Fig. 5, middle row), indicating a corresponding rise in the depth of each dimple (shadow area, in mm^2 , is a nearly perfect linear correlate of dimple depth, in mm: for a 13.8 mm length of hydrophobic wire, for example, $\text{area} = 34.6 \text{ depth} - 6.2$, $n = 8$, $r^2 = 1.00$). For the two smallest spiders (a, b), the horizontal acceleration was also accompanied by a distinct rise in body pitch (the angle between the animal's body and the water surface), but such an association was much less evident for the largest spider (c) (Fig. 5, bottom row).

Data from an earlier study indicated that leg length in these spiders is directly proportional to the log of mass (Fig. 6, modified from Suter & Wildman 1999, fig. 7A) and that the log of the angular velocities of the propulsive legs is

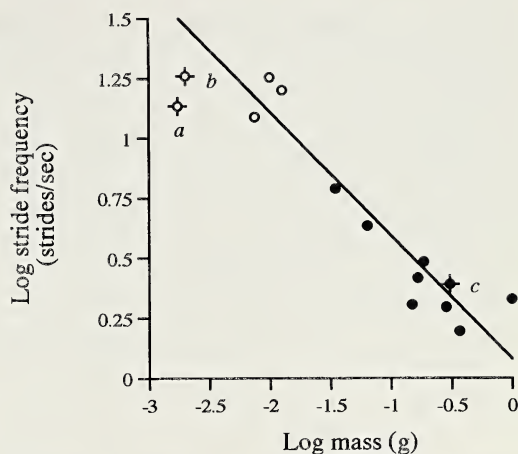


Figure 4.—Stride frequency during rowing is closely related to spider mass. A linear fit to log-transformed data yields the equation $\text{Log}_{10}f_s = -0.432 \text{ Log}_{10}m + 0.145$ ($n = 13$, $r^2 = 0.877$, $P < 0.01$). When we removed spiders smaller than 0.03 g from the analysis, the slope of the linear fit changed to -0.357 ($n = 9$, $r^2 = 0.676$, $P < 0.01$).

inversely proportional to the log of mass (Fig. 7, modified from Suter & Wildman 1999, fig. 7B). Further analysis of these data relating angular velocity to mass indicates that maximum (i.e., achievable) angular velocity is probably also a linear function of mass when both variables are log-transformed, but with a more steeply negative slope (Fig. 7). Because the propulsive force available during rowing is strongly dependent on the velocity of the leg tips, we used the equations relating mass to leg length and angular velocity (Figs. 6, 7) to elucidate the relationship between leg tip velocity and spider mass (Fig. 8). Achievable leg tip velocity rose steeply with mass until it reached its maximum at about 0.8 m/s in 33 mg spiders, and then fell with further increases in mass. In contrast, average leg tip velocity also rose rapidly to its peak (about 0.3 m/s) in 141 mg spiders but then declined only very slightly with further increases in mass.

DISCUSSION

General observations.—The principles governing the relationships between size and locomotion remain controversial despite several decades of careful measurements (reviewed, for example, in Peters 1983; Garland 1983; Calder 1984; Pennycuik 1992). Much of the controversy revolves around the scaling

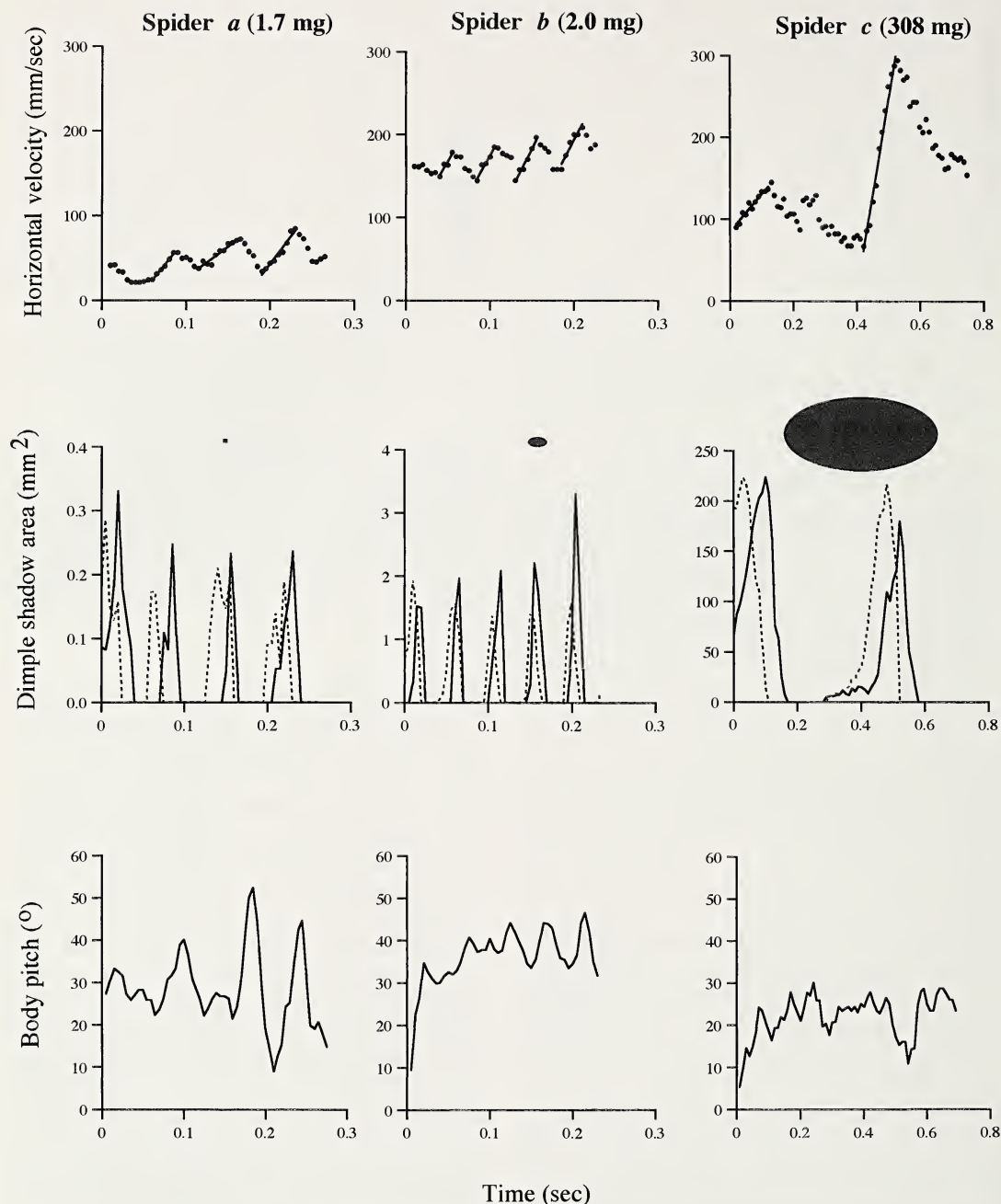


Figure 5.—Analysis of the rowing locomotion of the three spiders first identified in Figure 2. Velocities (top row of graphs; three-point running averages) vary periodically with time, indicating accelerations and decelerations that correspond to the propulsive and the glide phases of each rowing stroke; the horizontal acceleration during each stroke was calculated as the slope of the velocity versus time segment of the propulsive phase. The change in dimple shadow area (middle row of graphs) created by legs II (solid lines) and III (dashed lines) during the strokes graphed in the top row; ellipses indicate the relative sizes of maximum dimple shadows for the three different spiders. The change in body pitch (bottom row of graphs) during the same strokes; body pitch, referring to the angle formed between the body's long axis and the horizontal, varied substantially more during rowing by spider *a* than it did during the rowing of the other two spiders.

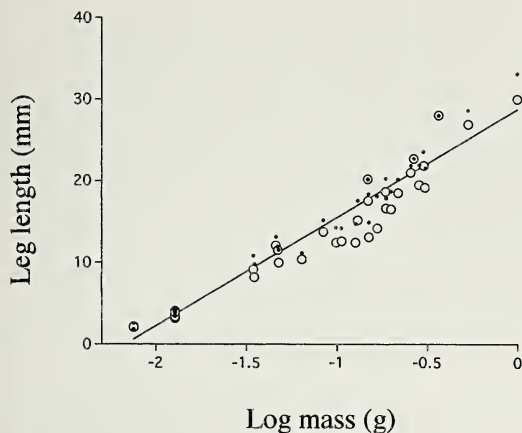


Figure 6.—Leg length in fishing spiders varies linearly with the log of mass. This relationship [$L_1 = 13.22 \text{ Log}_{10}m + 28.73$; $n = 62$, two legs each (● and ○) for 31 spiders, $r^2 = 0.946$, $P < 0.001$] is surprising because, for most other organisms in which it has been measured, it is the log-log relationship that is linear.

parameter that is to be held constant while other parameters are changed: different predictions follow from models based on geometric similarity, for example, than from those based on similarity of musculoskeletal elasticity or stress in the propulsive limbs. Not surprisingly, the reviewed literature concerns terrestrial locomotion, flying, and swimming, and ignores locomotion on the water surface. The present paper is the first to explore these relationships in an organism that regularly inhabits the water surface, although size and locomotion on the water surface by basilisk lizards has received some attention (Glasheen & McMahon 1996a, 1996b).

A comparison of the results of this study with expectations from other (principally vertebrate) studies reveals that models based on geometric similarity (Hill 1950) work well for rowing locomotion as performed by *D. triton* (Table 1): absolute velocity is approximately scale-invariant (Fig. 2) while relative velocity varies with $\text{mass}^{-0.31}$ (Fig. 3) and stride frequency varies with $\text{mass}^{-0.43}$ (Fig. 4). The absolute vs. relative velocity findings are particularly interesting for two reasons. First, the fact that very small spiders can achieve the same rowing velocities as adults despite a 610-fold difference in mass is remarkable. That achievement is made possible by both the rapid rise in stride frequency with decreas-

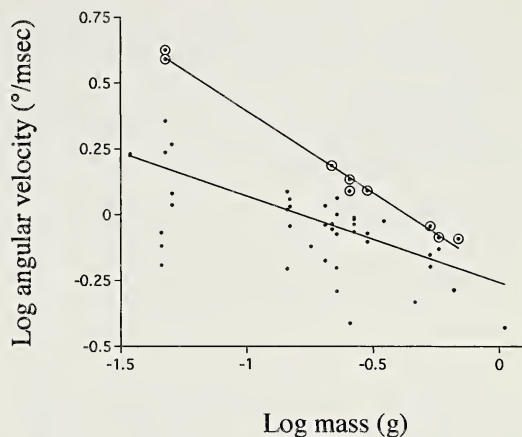


Figure 7.—Log-transformed angular velocities of the propulsive legs vary approximately linearly with the log-transformed masses of the spiders ($\text{Log}_{10}\omega = -0.328 \text{ Log}_{10}m - 0.256$, $n = 50$, $r^2 = 0.379$, $P < 0.01$). In an effort to estimate the angular velocities of which spiders are capable, we fit a line to the maxima (circled data points; $\text{Log}_{10}\omega = -0.623 \text{ Log}_{10}m - 0.266$; $n = 9$, $r^2 = 0.991$, $P < 0.01$).

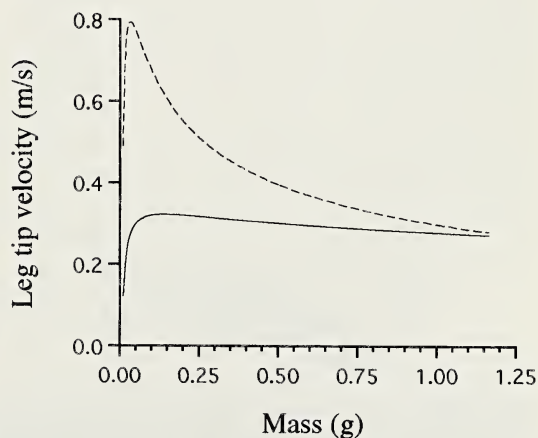


Figure 8.—Leg tip velocity is maximum when spiders are very small. The relationship between leg tip velocity and mass was calculated from the allometric relationships between leg length and mass (Fig. 6) and between leg angular velocity and mass (Fig. 7). The solid line indicates the relationship based upon average angular velocities (lower curve fit, Fig. 7) and the broken line indicates the relationship based upon maximum angular velocities (upper curve fit, Fig. 7). Peak leg tip velocities occurred at 0.141 g and 0.033 g for the solid and dashed lines, respectively.

Table 1.—Allometric relationships predicted in the literature and determined in this study.

Relationship	Proportionality			
	Expected	Source	Observed	Source
absolute velocity vs. mass	$V \propto m^0$	Hill 1950	$V \propto m^{0.02}$	Fig. 2
	$V \propto m^{0.24}$	Heglund et al. 1974		
relative velocity vs. mass	$V \propto m^{-0.33}$	Hill 1950	$V \propto m^{-0.31}$	Fig. 3
	$V \propto m^{-0.09}$	Calder 1984		
stride frequency vs. mass	$f_s \propto m^{-0.33}$	Hill 1950	$f_s \propto m^{-0.43}$	Fig. 4
	$f_s \propto m^{-0.17}$	Alexander 1982		

ing size (Fig. 4) and the fact that leg tip velocity is at a maximum in very small spiders (Fig. 8). The achievement also bespeaks the efficacy of the drag-based propulsive system used by even the smallest of the spiders (Suter & Wildman 1999). And second, relative velocity may be a better predictor of success at evading predation than is absolute velocity (Van Damme & Van Dooren 1999), hypothetically making newly hatched spiderlings far more difficult to capture than their parents since the spiderlings' relative velocities can be up to 10× as great (Fig. 3).

Conspicuous differences among small spiders.—The generalizations discussed above ignore the conspicuously poor performances of the two very small spiders with average rowing velocities < 0.05 m/sec (Fig. 2).

To understand their relative deficit, we analyzed one of them (Figs. 2–4) in detail, and compared the results to those of a similarly small but fast spiders (*b*) and to those of a much larger adult (*c*). In theory, the low velocity of *a* could be caused by any number of physiological or biomechanical deficits such as low power output by the muscles that move the legs, low stride frequency due to muscular or neural deficits, sub-optimal stroke direction, and so forth.

The difference between *a* and *b* in stride frequency (Figs. 4, 5), although in the right direction, is only about 12%, far too little to account for the more than three-fold difference in absolute velocity (Fig. 5, top row: *a*, 0.046 m/s; *b*, 0.16 m/s). In contrast, there are substantial and revealing differences between

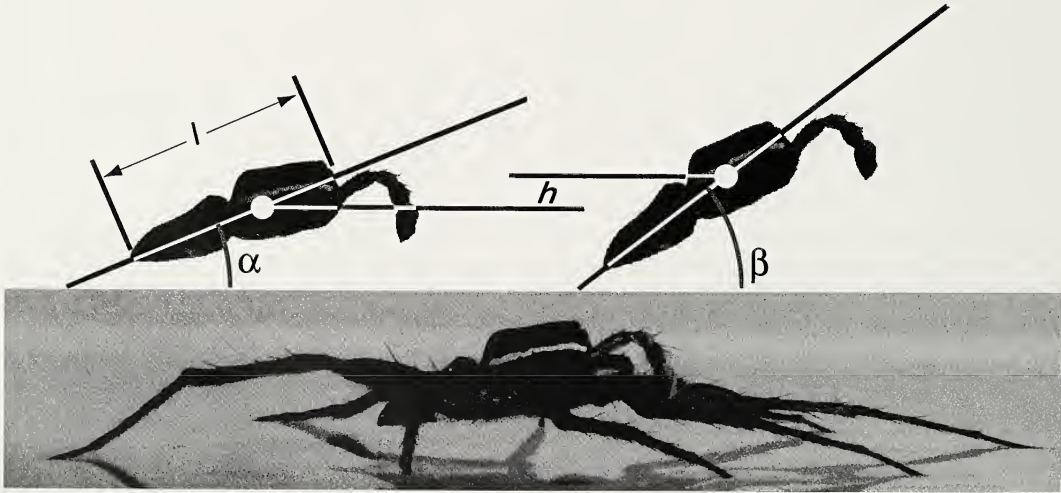


Figure 9.—The change in pitch of the long axis of the spider's body was measured both at the beginning of the rowing stroke (angle α) and at the peak of thrust production (angle β). The change in pitch allowed us to estimate the change in height of a spider's center of mass [$h \propto l (\sin \beta - \sin \alpha)$ where l is the length of the body] and therefore to calculate the vertical work done during the rowing stroke. Because a spider can raise its body without changing the body's pitch (Suter 1999), the use of pitch changes to estimate work done against gravity underestimates vertical work.

the dimple areas recorded during the power strokes of the three spiders in this comparison (Fig. 5, middle row): the 308 mg spider (*c*) made dimples in the water surface that were approximately 100 \times as large (in the horizontal plane) as those of the 2.0 mg spider (*b*), but this 2.0 mg spider's dimples were about 10 \times as large as those of the 1.7 mg spider (*a*). Because *a* is the outlier in performance (Fig. 2), we took the relationship between spider mass and dimple area to be best indicated by the data from *b* and *c*. From that perspective, the dimple area of *a* is low by a factor of between 7 and 8 (expected maximum dimple area, 2.01 mm²; observed maximum dimple area, 0.26 mm²).

Because the relationship between dimple area and dimple depth is linear (see Results), the observed deficit in dimple area for *a* corresponds to a seven- to eight-fold deficit in dimple depth. That difference, in turn, is more than enough to account for the observed velocity difference between spiders *a* and *b*, because the horizontal thrust force that can be generated by a spider on the water surface is strongly influenced by dimple depth (Suter et al. 1997; Suter & Wildman 1999). To spider *a*, therefore, the water surface would appear to be very slippery, offering much less resistance to the backward motion of the propulsive legs than would be encountered if the dimples were deeper. The spider could compensate behaviorally for the deficit in dimple depth (and resistance) in either of two ways: it could increase the angular velocities of the propulsive legs or it could deflect some of its leg displacement downward in an attempt to increase dimple depth, either of which would have the effect of increasing drag (Suter & Wildman 1999). Our estimates of the ratios of vertical to horizontal work during rowing strokes (Fig. 10, derived from pitch measurements like those in Fig. 5, bottom row) indicate that spider *a* was doing about four times as much work to raise itself against gravity as it was to propel itself forward, confirming its attempts to increase dimple depth. Not surprisingly, the spider with the highest ratio of vertical to horizontal work, *d* (Fig. 10), was also very small and the slowest of all of the spiders tested (Fig. 2).

The underlying cause of the difference in dimple sizes that appears to be at the root of the locomotor difficulties experienced by spi-

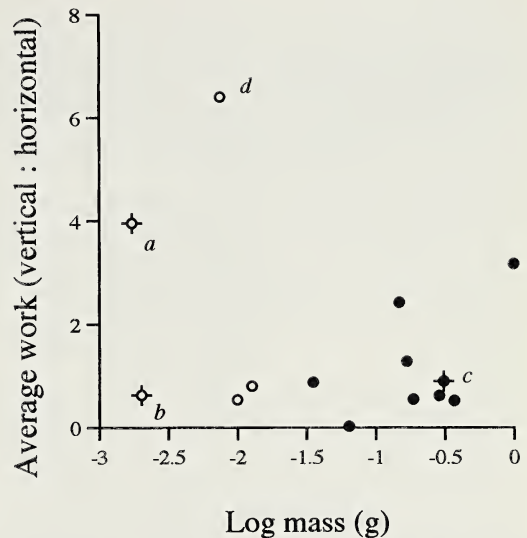


Figure 10.—The ratio of vertical work ($w = mgh$, mJ) to horizontal work ($w = mad$, mJ) in relation to the log of spider mass. The high ratio measured for spider *a* (four times as much work going into vertical displacement as into horizontal locomotion during each rowing stroke) provides an explanation for the conspicuously slow horizontal locomotion of that spider (Fig. 2). That inefficiency is surpassed by only one spider (*d*), which is similarly conspicuous in horizontal velocity (Fig. 2, lowest velocity).

der *a* but not by spider *b* remains obscure. Because the two spiders differed little in mass (1.7 vs. 2.0 mg), the mass difference is unlikely to explain the differences in dimple sizes. We suspect, instead, that variations either in the hydrophobicity of the spider cuticle or in the structures of hairs on the tarsi (J. Rovner and P. Sierwald, pers. comm.) may account for the unexplained differences.

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Appendix 1.—Symbols used in the text and figures.

Symbol	Meaning	Units
<i>a</i>	acceleration	m/s ²
<i>d</i>	distance	m
<i>F</i>	force	mN
<i>f_s</i>	stride frequency	strides/sec
<i>g</i>	acceleration due to gravity	m/s ²
<i>h</i>	height	m
<i>l</i>	length of body	m
<i>m</i>	mass	g
<i>P</i>	pitch of longitudinal axis	degrees
<i>V_{rel}</i>	relative velocity	body lengths/sec
<i>w</i>	work	mJ

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CHEMICAL CUES FROM ANTS INFLUENCE PREDATORY BEHAVIOR IN *HABROCESTUM PULEX*, AN ANT-EATING JUMPING SPIDER (ARANEAE, SALTICIDAE)

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ABSTRACT. The ability of *Habrocestum pulex*, a myrmecophagic jumping spider, to detect olfactory and contact chemical cues from ants was investigated experimentally. When given a choice between walking over clean soil or soil that had housed ants, *H. pulex* spent significantly more time on ant-treated soil. However, *H. pulex* did not appear to discriminate between clean blotting paper and blotting paper over which ants had walked. In tests using a Y-shaped olfactometer, when given a choice between an experimental arm containing air from a cage containing ants, or 6-methyl-5-hepten-2-one, and a control arm containing clean air, *H. pulex* moved into the experimental arm significantly more frequently than the control arm. When on soil that had previously housed ants, agitated walking, undirected leaping, posturing with body raised, and perching on top of corks were each significantly more prevalent than when *H. pulex* was on clean soil. Chemical cues left by ants on soil also affected *H. pulex*'s attention to visual cues from ants: when on treated soil, *H. pulex* initiated and completed stalking sequences more often, and after shorter latency, than when on control soil.

Keywords: Prey detection, myrmecophagy, kairomone, Salticidae, *Habrocestum pulex*

Unique, complex eyes and acute vision in jumping spiders (Salticidae) have led to the evolution of intricate, vision-guided courtship and predatory tactics (Crane 1949; Drees 1952; Land 1969a, 1969b; Forster 1982; Blest et al. 1990; Jackson & Pollard 1996, 1997). However, salticids are not restricted to reliance on optical cues, as tactile, auditory and substrate-vibration cues also influence salticid courtship, either concurrent with or as alternatives to, visual communication (Richman & Jackson 1992; Jackson & Pollard 1997). Pheromone-based intraspecific communication is also widespread in the Salticidae (Crane 1949; Jackson 1987; Pollard et al. 1987; Willey & Jackson 1993; Clark & Jackson 1994a, 1994b, 1995a, 1995b), but little is known about whether salticids are influenced by kairomones (chemicals that provoke a response beneficial to the receiver but not the sender of the signal, where the sender and receiver belong to different species; Brown et al. 1971).

Ants are one of the most abundant prey-size arthropods in the habitats of most spiders (Hölldobler & Wilson 1990), but their defenses (strong mandibles, formic acid and poison-

injecting stings: Wray 1670; Edmunds 1974; Hölldobler & Wilson 1990; Blum 1992) appear to present spiders with formidable challenges. Yet a minority of spiders has overcome the ant's defenses, thereby gaining access to this exceptionally numerous prey (Mackay 1982; Oliviera & Sazima 1985; Nyfeler et al. 1988; Elgar 1993; Cushing 1997).

Within the Salticidae, 21 ant-eating (myrmecophagic) salticids have been studied in detail: *Aelurillus aeruginosus* (Simon 1871), *A. cognatus* (O.P.-Cambridge 1872), *A. kochi* Roewer 1951, six undescribed species of *Chalcotropis* Simon 1902, *Chrysilla lauta* Thorell 1887, *Corythalia canosa* (Walckenaer 1837), *Habrocestum pulex* (Hentz 1846), *Siler semiglaucous* Simon 1901, *Siler* sp. Simon 1889, three undescribed species of *Natta* Karsch 1879, two undescribed species of *Xenocytaea* Berry, Beatty, Prózyński 1998 (formerly called "*Euophrys*") and *Zenodorus orbiculatus* (Keyserling 1881) (Edwards et al. 1974; Cutler 1980; Jackson & van Olphen 1991, 1992; Li et al. 1996, 1999; Jackson et al. 1998). Although these species feed on a wide variety of insects, they have all been

shown in standardized tests to prefer ants over other prey and to have ant-specific prey-capture behavior (Li & Jackson 1996). Except for *Corythalia canosa* and *Zenodorus orbiculatus*, each of these species has been shown to prefer ants as prey and to use ant-specific prey-capture behavior even when tested with motionless lures (dead insects mounted in life-like posture on corks), implying that optical cues pertaining to shape and form enable them to distinguish ants from other insects (Li & Jackson 1996; Li et al. 1996; Jackson et al. 1998). However, the ability to rely solely on vision for detecting ants does not preclude the possibility that chemical cues also influence the predatory behavior of myrmecophagic salticids.

In the present paper, we investigate how *Habrocestum pulex*, a previously studied myrmecophagic salticid from North America, responds to chemical cues from ants. *Habrocestum pulex* lives in leaf litter, a microhabitat in which numerous visual obstructions might often hinder early visual detection of prey. Ability to detect chemical cues from ants might play an important role in preparing *H. pulex* to respond appropriately to its unusually dangerous prey.

In earlier studies (Cutler 1980; Li et al. 1996), *H. pulex* was tested with prey in a simple laboratory environment. In the present study, we first observe *H. pulex*'s predatory behavior in an environment with leaf litter present, thereby simulating nature more closely than previously. We next consider three hypotheses concerning how *H. pulex* might react to contact chemical cues when in an environment recently occupied by ants. *Habrocestum pulex* might do any combination of the following: remain in the environment, adopt behavior and posture appropriate for capturing ants, or exhibit heightened attention to optical cues from ants. We consider the role of both olfactory and contact chemical cues from ants in moderating the prey-capture behavior of *H. pulex*.

METHODS

General.—Except for minor modifications, maintenance procedures, cage design and data analysis were as in earlier studies (Jackson & Hallas 1986). All experiments were carried out in New Zealand using laboratory cultures of *H. pulex*, originally collected in Kansas,

USA. Each individual salticid was used in a maximum of two tests for any one experiment, and there was no evidence that the identity of individual salticids influenced test outcome. Data from males and females, not being statistically different, were pooled. Body lengths of adults were 3–5 mm. Statistical methods were from Sokal & Rohlf (1995).

In observations and experiments with live ants, we used *Monomorium antarcticum* Smith 1858, a myrmicine ant native to New Zealand (Ettershank 1966; Bolton 1987). The most common prey of *H. pulex* in nature appear to be *Lasius* spp. Fabricius 1804 (Formicinae) (Cutler unpubl. data), which were not available in New Zealand. To test for responses which might be specific to *Lasius* spp., we conducted olfactometer tests using commercially available 6-methyl-5-hepten-2-one (Sigma Chemical Co.), an alarm pheromone of *Lasius* spp. and other ants (Duffield et al. 1977; Blum 1981; Türker 1997a, 1997b). *Monomorium antarcticum* and other myrmicine ants appear not to make this pheromone (Hölldobler & Wilson 1990).

Predation on ants in a complex environment.—The environment was a plastic box (length 170 mm, width 110 mm, depth 60 mm) filled to a depth of 15 mm with soil. Leaf litter was scattered about on top of the soil, covering about 30% of the box surface. Four small corks on which *H. pulex* could stand were spaced within the box, providing perches above the level of leaf litter. Observations were staged by putting *H. pulex* in this environment in the presence of 10–20 prey, where (depending on the test) prey were either ants or vestigial-winged fruit flies (*Drosophila melanogaster* Meigen 1804). The goal was to get qualitative information on how *H. pulex* captured prey in approximately natural environments.

Choice tests using blotting paper.—We adopted, after minor modification, procedures devised earlier for testing the ability of salticids to discriminate between the draglines of different conspecific individuals (Clark & Jackson 1994a, 1995a, 1995b). In each test, *H. pulex* was offered a choice between treated (had been in contact with ants) and untreated (clean) blotting paper. Treated blotting paper was prepared by leaving four ants in a plastic petri dish (diameter 90 mm) for two hours, with one circular piece of blotting paper taped

to the top and another to the bottom. During the two-hour period, ants actively walked about in the petri dish, repeatedly moving over both pieces of blotting paper.

Immediately afterward, each piece of blotting paper was cut in half and the test chamber was prepared. The test chamber was another petri dish (diameter 90 mm) with one half piece of treated blotting paper taped to the top of the dish and another half-piece of treated blotting paper taped to the bottom of the dish directly below the top piece. The other half of the test chamber had control blotting paper taped to the top and bottom. A 15-mm triangle, cut out of the blotting paper and surrounded by a horseshoe-shaped metal divider, served as a "neutral area" into which the test spider was introduced before testing. Having the metal divider in place meant that the salticid could not, all at once, view the entire space within the petri dish (see Clark & Jackson 1994a). A test was defined as having started when the spider moved out of the neutral area and onto the blotting paper. This always happened within 1 min. The test ended 10 min later. For each test, a difference score was obtained (time spent on treated paper minus time spent on control paper). Maximum and minimum possible scores were +600 sec (spent entire time on ant-treated blotting paper) and -600 sec (spent entire time on control blotting paper), respectively.

Choice tests using soil.—Commercial potting mix was placed in a square (160 mm × 160 mm, height 80 mm) plastic storage container filled to a depth of 20 mm and microwaved (900 W) for 10 min, then held in the container (kept closed) for a waiting period of 20–30 days. Treated soil was prepared by keeping about 100 ants in the closed container during the waiting period. Potential contaminants from feeding material were avoided by not feeding the ants during this time. The ants survived the fasting period. Control soil was kept ant free.

The test chamber was a plastic box (length 170 mm, width 110 mm, height 60 mm) filled to a depth of 15 mm with control soil. Two watch glasses (inner diameter 50 mm, inner height 7 mm; outer diameter 65 mm, outer height 15 mm) were placed 10 mm apart (measured from nearest edges) in the center of the box. The watch glasses were filled with soil, then embedded in the surrounding soil

(soil level with rim of watch glass). To facilitate seeing whether test spiders were in the watch glass, the rim of each glass was kept clear of soil. Treated soil was placed in the experimental watch glass (ants removed immediately beforehand) and control soil was placed in the control watch glass. Whether treated soil was on the left or right was decided at random for each test. To start a test, a spider was placed on the soil between the two watch glasses. For the next 60 min, we recorded how much time the test spider spent in each watch glass. Time spent outside the watch glasses was ignored.

Effect of chemical cues in soil on behavior and posture.—Control and treated soils were prepared as in the experiment on choice of soil. Each test spider was tested on one day with treated soil and on the previous or next day (order decided at random) with control soil. During 15-min tests, the test spider's behavior was recorded in detail, but we present data here only where there was statistical evidence of behavior being influenced by soil treatment.

The test chamber was a cylindrical plastic dish (diameter 90 mm, height 40 mm) with soil covering the bottom to a depth of 10 mm. Four corks (diameter 9 mm at the narrow end) were embedded with the upper 5 mm of cork (narrow end) extending above the soil. Corks were evenly spaced in a square centered in the middle of the dish (center of each cork 20 mm from the center of the nearest neighboring cork). Evenly spread around the dish between the corks were four convex 10 × 10 mm pieces of leaf litter (Oak, *Quercus* spp. Linnaeus 1753), each positioned so that the test spider could walk under it.

Effect of chemical cues in soil on attention to optical cues.—We investigated whether *H. pulex*'s attention to optical cues from ants is affected by the presence of chemical cues from ants. Preparation of soil and the test chamber was as described for the experiment on how chemical cues affect behavior and posture, except that no leaf litter was present and there was a glass vial (65 mm long, inner diameter 10 mm) containing two ants on the soil centered between the corks. Latencies to initiate and complete stalking sequences directed at the ants were recorded. Stalking was initiated when the test spider turned toward an ant and began to move steadily toward it, and

completed when the test spider touched the vial. Test spiders were allowed 15 min to begin stalking and subsequently allowed 15 min to complete the stalking sequence.

Olfactometer tests.—A Y-shaped olfactometer (Fig. 1) with airflow adjusted to 1000 ml/min (Matheson FM-1000 flowmeter) was used to assess *H. pulex*'s response to airborne odors from ants. At this airflow setting, there was no evidence that *H. pulex*'s locomotion was impaired. Air flowed from a tap through two separate flowmeters into a stimulus chamber (which contained an odor source) and a control chamber (which was empty). During experimentation, whether the experimental chamber was on the left or right side of the olfactometer was decided at random. Air moved from the stimulus chamber to the stimulus arm and from the control chamber to the control arm. Collectively, the stimulus and control arms are referred to as the "choice arms." Air flowed from each "choice arm" into a single test arm. At one end of the test arm, there was a holding chamber into which a spider was placed prior to testing. A metal barrier, positioned in a slit between the holding chamber and the test arm, blocked the spider's entry into the test arm. Thirty min before each test, an odor source (depending on the experiment, either four ants or 10 μ l of 6-methyl-5-hepten-2-one) was placed in the experimental chamber. This 30-min period allowed the air to circulate evenly and ensured that air pressure was comparable throughout the olfactometer.

During testing, spiders tended to walk about actively in the olfactometer, sometimes entering the experimental or control arm, or both, several times but staying only briefly. For each spider, we recorded both the first and final choice. The first arm the spider entered was its first choice regardless of how long it stayed. By definition, a spider made its final choice when it entered an arm and remained there for a minimum of 30 sec. A maximum of 60 min was allowed for the spider to make a final choice after leaving the holding chamber. Between tests, the olfactometer was dismantled and cleaned first with 80% ethanol and then with water. This was a precaution against the possibility that spiders might be affected by draglines or chemical traces from previously tested spiders.

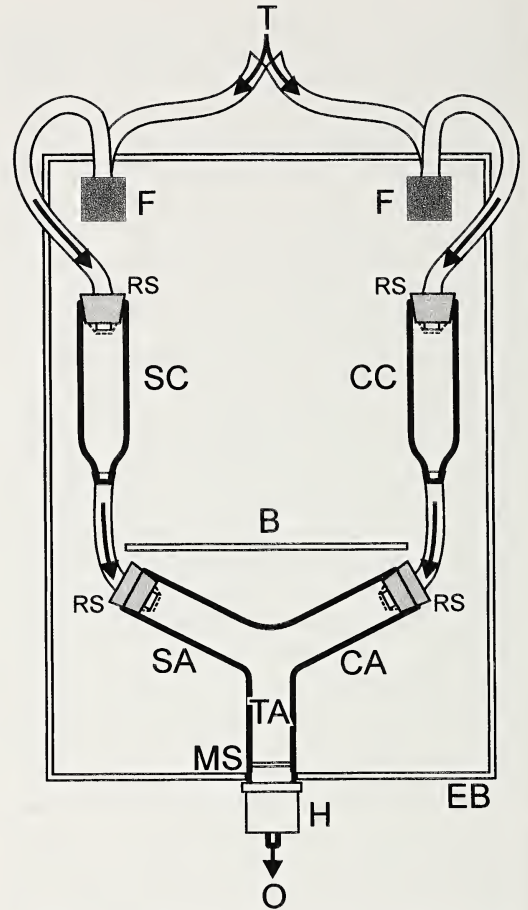


Figure 1.—Olfactometer. Arrows indicate direction of airflow. SC = stimulus chamber (contains odor source); CC = control chamber (empty); H = holding chamber (location of test spider at start of test); TA = test arm; CA = control arm; SA = stimulus arm; MS = metal screen fitted in slit (blocks spider's entry into test arm before test begins); T = tap from which air enters olfactometer; B = opaque barrier (prevents test spider from seeing ants); RS = rubber stopper; O = air leaves olfactometer; EB = edge of box enclosing olfactometer. Diagram not to scale. See text for details.

RESULTS

Predation on ants in a complex environment.—*Habrocestum pulex* tended to leap on fruit flies from any orientation, but attacked ants by repeatedly approaching head on, making stabs with its fangs, then backing away (Fig. 2). Once the ant was more or less quiescent, *H. pulex* approached slowly, grasped the ant and began feeding. During and immediately prior to attacking an ant, the spi-

der's palps were retracted to the sides of the chelicerae, but palps tended not to be retracted during attacks on flies.

Locomotion, when it occurred during tests with flies, tended to be by slow, continuous stepping, and the normal posture was adopted with the body *ca.* 1 mm above the substrate and legs only moderately extended. With ants, prey-capture sequences were normally preceded by distinctive preliminary behavior which included agitated walking, undirected leaping and posturing with the body raised. These sequences were often preceded by periods during which *H. pulex* simply watched (maintained orientation towards) an ant. Agitated walking was a distinctive style of motion in which *H. pulex* repeatedly spurted forward for *ca.* 0.5 sec at 30–50 mm/sec, paused and then spurted forward again. *Habrocestum pulex* made undirected leaps by suddenly propelling itself more or less straight upward with no target being evident. When in the body-elevated posture, *H. pulex* stood with its legs more extended than normal, so that its body was 2–3 mm off the substrate.

When predation was delayed or failed to occur in tests with flies, *H. pulex* spent much of the time sheltering under leaf litter, but *H. pulex* rarely sheltered under leaves in tests with ants. A common preliminary to predation on both ants and flies was for *H. pulex* to stand on corks and watch prey active on the soil below (Fig. 3). Attacks were often made by rushing down from a cork, after which *H. pulex* usually returned to the top of the same cork to feed.

Choice tests using blotting paper.—Scores were spread more-or-less evenly over the range of possible values, providing no evidence that *H. pulex* discriminated between treated and control blotting paper (Fig. 5).

Choice tests using soil.—*Habrocestum pulex* spent more time on treated, rather than control, soil (Fig. 6). In 20 tests, one spider spent more time on control soil, one spent equal time on treated and control soil, and the remaining 18 spent more time on treated soil (McNemar test comparing the number that spent more time on treated versus control soil; $P < 0.001$, $n = 19$).

Effect of chemical cues in soil on behavior and posture.—Agitated walking, undirected leaping, the body-raised posture and perching on corks were more prevalent when

H. pulex was in experimental chambers rather than control chambers (Table 1).

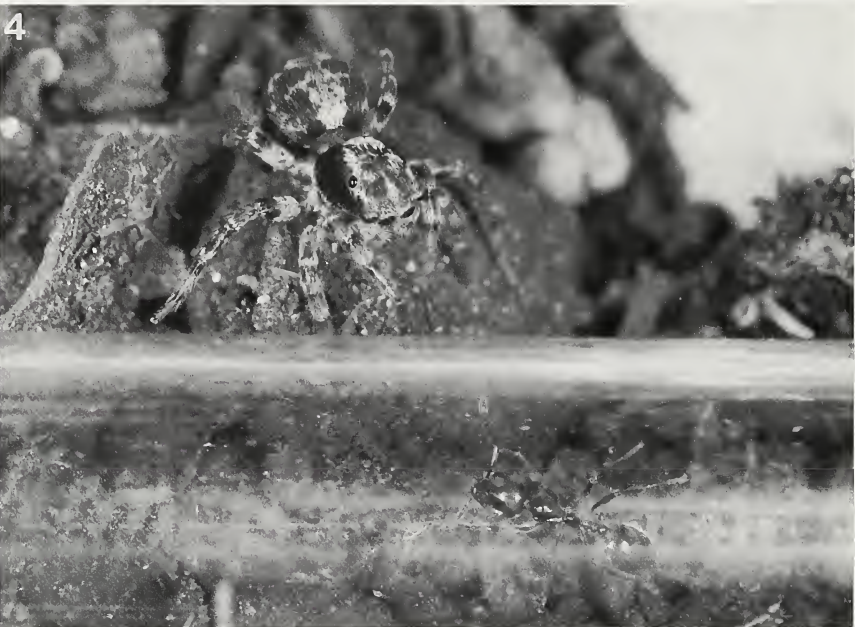
Effect of chemical cues in soil on attention to optical cues.—When on treated soil, *H. pulex* initiated and completed (Fig. 4) stalking sequences against ants more often than when on control soil (Table 1). The latency to initiate and to complete stalking was shorter on treated than control soil (Fig. 7).

Olfactometer tests.—When tested with ants in the stimulus chamber, the first choice was the stimulus arm in 11 tests and the control arm in four tests (binomial, NS). The final choice was the stimulus arm in 13 tests and control arm in two tests (binomial, NS). In all tests in which the stimulus arm contained 6-methyl-5-hepten-2-one, the first and final choices were identical: the stimulus arm in 10 tests and the control arm in one test (binomial, NS). There was no statistical evidence of a relationship between latency to choose and whether the choice was the control or the stimulus arm or, if it was the stimulus arm, whether the stimulus was pheromone or an ant (Mann-Whitney rank-sum tests, NS; Fig. 8).

DISCUSSION

Habrocestum pulex apparently detects and responds adaptively to chemical cues from ants. Our findings support the following hypotheses: (1) *H. pulex* chooses to remain on soil containing chemical cues from ants (choice of soil); (2) ant-derived chemical cues in soil stimulate *H. pulex* to adopt posture and behavior appropriate for capturing ants, even in the absence of optical cues from ants (effect of chemical cues on behavior and posture); (3) ant-derived chemical cues in soil heighten *H. pulex*'s attention to optical cues from ants (effect of chemical cues in soil on attention to optical cues); and (4) *H. pulex* is attracted by olfactory cues from ants (olfactometer tests). Failure to show a preference for treated over control blotting paper in a petri dish suggests that blotting-paper choice tests are excessively artificial.

Rather than demonstrating responses to the particular ant species on which *H. pulex* preys most often in nature, our results suggest that *H. pulex* has evolved the ability to detect and respond adaptively to chemicals secreted by a broader range of ants. In all experiments, we used *Monomorium antarcticum*, a New Zealand myrmicine ant which would not be en-



Figures 2-4.—2. *Habrocestum pulex* (on right) slowly approaches ant (*Monomorium antarticum*) (on left). Ant now quiescent, having been repeatedly stabbed by *H. pulex*; 3. *Habrocestum pulex* on top of cork watching ant (not in photograph) moving about on soil; 4. *Habrocestum pulex* completes stalking sequence in tests of effect of chemical cues in soil on attention to optical cues (see text). Ant in glass vial (lower right). *H. pulex* (above, left) faces ant and touches glass.

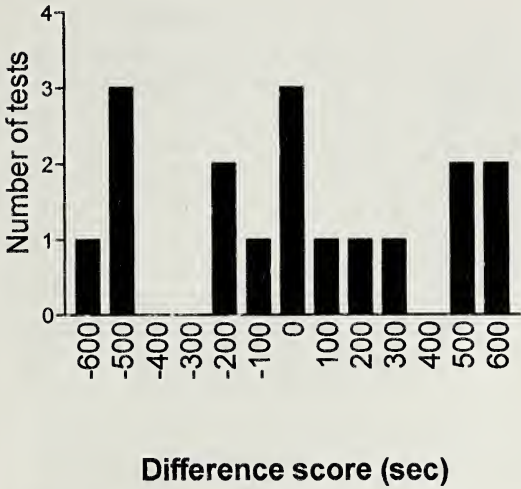


Figure 5.—Distribution of difference scores (time spent on treated blotting paper minus time spent on control blotting paper) from experiment on choice of blotting paper. See text (data more-or-less evenly spread). No statistical evidence of preference (Wilcoxon test for paired comparisons, NS).

countered by *H. pulex* in nature. *Habrocestum pulex* preys especially often in nature on *Lasius* spp., which are formicines. In our experiments, *H. pulex* also was influenced by 6-methyl-5-hepten-2-one, a ketone characteristic of the mandibular gland secretions of many formicine ants and the anal gland secretions of dolichoderine ants (Duffield et al. 1977). In ants, use of chemically-similar pheromones by different species is common (Gabba & Pavan 1970).

The ketone 6-methyl-5-hepten-2-one ap-

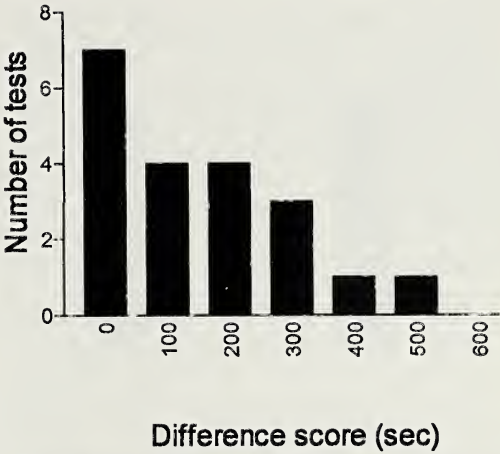


Figure 6.—Distribution of difference scores (time spent in experimental watch glass minus time spent in control watch glass) from experiment on choice of soil, showing preference for treated soil (Wilcoxon test for paired comparisons, $P < 0.001$). Note: There was only one negative score.

pears to be a kairomone not only for *H. pulex* but also for *Habronestes bradleyi* Walckenaer, a myrmecophagic zodariid spider. When tested in a Y-shaped olfactometer, with a choice between chemical cues from disturbed dolichoderine ants (*Iridomyrmex purpureus* Smith 1858) and clean air, *Habronestes bradleyi* most often moved toward the cues from injured or disturbed ants (Allan et al. 1996). Gas chromatography revealed that 6-methyl-5-hepten-2-one is released in high concentrations by injured or disturbed *Iridomyrmex purpureus*. When retested in the Y-shaped ol-

Table 1.—Results from experiments on effects of chemical cues in soil on *Habrocestum pulex*. A. Behavior and posture. B. Attention to optical cues. Each spider tested one day on treated soil (had been in contact with ants) and on alternate day on control soil (had not been in contact with ants). Compared to when on control soil, *H. pulex* on treated soil: A. performed more agitated walking, undirected leaping, holding body raised and perching on wall. B. More often initiated and completed stalking. See text for details. Data analysis: McNemar test for significance of changes (for these tests, only the first two columns of data are used).

Experi- ment	Response	On treated soil only	On control soil only	On both types of soil	On neither type of soil	McNemar test
A	Agitated walking	8	1	9	2	$P < 0.05$
	Undirected leaping	12	1	2	4	$P < 0.01$
	Holding body raised	12	0	4	4	$P < 0.01$
	Perching on cork	11	1	5	3	$P < 0.01$
B	Initiate stalking	11	1	7	1	$P < 0.01$
	Complete stalking	12	2	4	2	$P < 0.01$

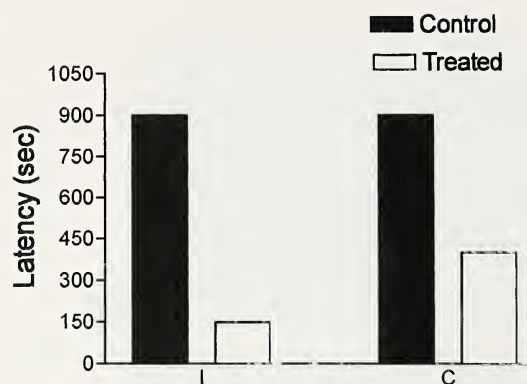


Figure 7.—Latencies (median in sec) to initiate (I) and complete (C) stalking sequence (see text for definitions) in experiment testing for effect of chemical cues in soil on attention to optical cues. Latencies when on treated soil (been in contact with ants) shorter than latencies when on control (clean) soil (Wilcoxon tests for paired comparisons, $P < 0.005$ for both initiating and completing stalking).

factometer, test spiders moved into olfactometer arms which contained 6-methyl-5-hepten-2-one more often than into the clean arms (Allan et al. 1996), implying that this ketone is at least one of the chemicals used by *Habronestes bradleyi* to locate *I. purpureus*.

Detecting 6-methyl-5-hepten-2-one is unlikely to be how *H. pulex* detects *Monomorium antarcticum*. Whether *M. antarcticum* uses alarm pheromones is unknown. Other myrmicine ants are known to do so, but they use another closely related ketone, 4-methyl-3-heptanone (Gabba & Pavan 1970; Hölldobler & Wilson 1990), instead of 6-methyl-5-hepten-2-one. It may be that, for myrmecophagic spiders and for ants, sensory systems are not narrowly tuned to particular ketones, but instead respond to a range of structurally related chemicals (see Türker 1997a, b). Perhaps, *H. pulex* has evolved chemoreceptors sensitive to a series of structurally related chemicals, rather than those secreted by any particular set of ant species. Broad-sensitivity sensors would assist *H. pulex* in predatory sequences against a wide range of ant species, including even New Zealand ants it would never encounter in nature.

Kairomone detection appears to function not only to bring *H. pulex* into proximity with its prey, but also to elicit changes in behavior, body posture and locomotion that prepare *H. pulex* for predation on ants before an ant is

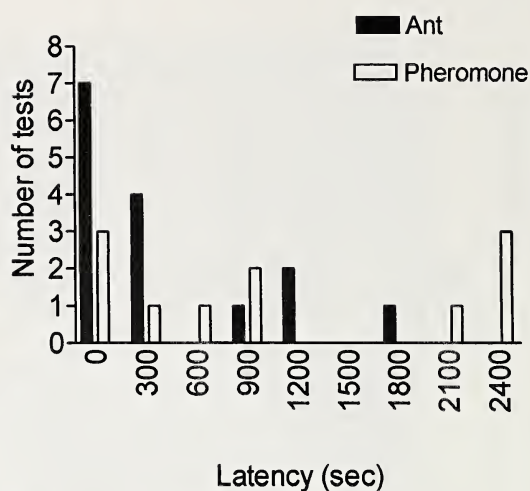


Figure 8.—Latency for test spiders to enter the experimental arm in olfactometer tests. Choice was between experimental arm (contained either live ants ("ant"; $n = 15$) or 6-methyl-5-hepten-2-one ("pheromone"; $n = 11$) or control arm. Instances of choosing control arm are not shown.

seen. In particular, cues from ants caused *H. pulex* to move to higher ground (i.e., perch on corks), where its ability to detect optical cues from ants might be enhanced; and *H. pulex* often launched attacks on ants from elevated positions.

Habrocestum pulex illustrates that the evolution of complex eyes and exceptionally intricate vision-based predatory behavior in salticids is not incompatible with the evolution of kairomone-detection abilities and intricate chemical-mediated predatory behavior in myrmecophagic salticids. In salticids, a vision-based perceptual and behavior system appears to have only minimal, if any, cost to proficiency at using a chemical-based perceptual and behavior system (Jackson & Pollard 1996, 1997). In *H. pulex*, the ways in which chemoreception influences predatory behavior are as intricate as those known for any non-salticid spider. Independently of optical cues, *H. pulex* not only appears to use kairomones for locating and preparing to prey on ants. Kairomones also appear to influence attention to optical cues. When ant-derived cues were present, *H. pulex* located ants faster than when they were absent. This suggests that the chemical and vision-based perceptual systems of salticids may have reached a remarkable level of integration.

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LIFE HISTORY OF *PARDOSA MOESTA* AND *PARDOSA MACKENZIANA* (ARANEAE, LYCOSIDAE) IN CENTRAL ALBERTA, CANADA

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ABSTRACT. The density, fecundity, and life-cycle of *Pardosa moesta* Banks 1892 and *Pardosa mackenziana* (Keyserling 1877) were studied in a deciduous forest in central Alberta, Canada. Density estimates were lower than reported for other *Pardosa* species; they ranged from 0.46 per m² for male *P. mackenziana* to 2.99 per m² for immature *P. mackenziana*. Adult female densities were below 1 per m² for both species. Clutch sizes were highly variable and averaged (\pm SE) 33.06 ± 1.29 for *P. moesta* and 48.37 ± 1.67 for *P. mackenziana*. Although clutch size was positively related to female size, little of the variation was adequately explained by female size alone. Several lines of evidence suggest that *P. moesta* and *P. mackenziana* require two years to mature in central Alberta, with a peak reproductive period in May and June. Females carry egg sacs into the summer months and immature spiders overwinter following the first growing season when they are still less than 5 mg in weight. After a second summer of growth, subadults overwinter and maturation occurs early in the spring.

Keywords: Lycosidae, density, fecundity, phenology, life-cycle

Wolf spiders in the genus *Pardosa* C.L. Koch 1847 are among the most conspicuous and abundant of the ground-dwelling spiders. However, little is known about the life history of many northern species of this genus in North America, even though 46 species are found in Canada, at least eight of which are distributed widely across the country (Dondale & Redner 1990). Two of these species, *Pardosa moesta* Banks 1892 and *Pardosa mackenziana* (Keyserling 1877), have been noted as being among the most abundant wolf spiders collected in deciduous forests of north-central Alberta (Buddle et al. 2000).

Significant progress has been made in understanding the ecology and biology of many *Pardosa* species in Europe, Japan, and southern latitudes in North America (e.g., Hallander 1967; Vlijm & Kessler-Geschiere 1967; Miyashita 1968, 1969; Edgar 1971a, b, 1972; Dondale 1977; Greenstone 1980; Orazé et al. 1989; Samu et al. 1998). It is commonly thought that most spiders living in temperate zones have annual life-cycles (Gertsch 1979), and this is true for many *Pardosa* from various regions including Europe, southern Canada, and the United States (Vlijm & Kessler-Geschiere 1967; Schmoller 1970; Dondale 1977; Orazé et al. 1989). However, several

Pardosa species studied from high altitudes, northern latitudes, and under cooler conditions require more than one year to complete their development (Leech 1966; Schmoller 1970; Edgar 1971b).

Other characteristics such as natural densities of *Pardosa* species and estimates of clutch size are known for many species in the United States and some regions in Canada (e.g., Eason 1969; Schmoller 1970; Dondale 1977; Lowrie & Dondale 1981), and various species from Europe (e.g., Edgar 1971b; Kessler 1971). For example, Dondale (1977) reported densities of *P. saxatilis* (Hentz 1844) between 0.8–4.4 per m² in southern Ontario; and as part of a detailed study of *P. lugubris* (Walckenaer 1802) in Scotland, Edgar (1971b) reported densities of various life stages between 1.7–6.2 per m². There is also a variety of published records on the average clutch size for many *Pardosa* species, and these range from as low as 25.5 eggs/female for the small species *P. saxatilis* to a high of 82.0 eggs/female for the larger *P. amentata* (Clerck 1757) (Marshall & Gittleman 1994).

During 1998 and 1999 I studied life history characteristics of *P. moesta* and *P. mackenziana*. The objectives were to determine the natural densities of these species, establish

their clutch sizes and assess whether the number of offspring is determined by female size, and to ascertain the life cycles of *P. moesta* and *P. mackenziana* in deciduous forests of central Alberta, Canada.

METHODS

Study site and species descriptions.—This work was done at the George Lake Field Site located 75 km northwest of Edmonton, Alberta (ca. 53°57'N, 114°06'W). There are approximately 180 ha of continuous hardwood forest at the field site, which is surrounded by agricultural land to the south and west, a lake to the east, and more than 500 ha of continuous deciduous forest to the north. Dominant tree species include trembling aspen (*Populus tremuloides* Michx.), balsam poplar (*Populus balsamifera* L.), birches (*Betula papyrifera* Marsh. and *B. neoalaskana* (Sarg.)), and patches of white and black spruce (*Picea glauca* (Moench) Voss and *P. mariana* (Mill.) BSP). The study area for this research was a 2.2 ha area of upland aspen forest (Niemelä et al. 1992).

Pardosa moesta and *P. mackenziana* are among the most abundant wolf spiders found on the forest floor at George Lake; other *Pardosa* species encountered less frequently include *P. xerampelina* (Keyserling 1877), *P. fuscata* (Thorell 1875), *P. distincta* (Blackwall 1846) and *P. ontariensis* Gertsch 1933. *Pardosa moesta* has general habitat affinities including meadows, hayfields, marshes, bogs, lawns, gravel pits, clear-cuts, rocky shores, and deciduous forests (Wolff 1981; Dondale & Redner 1990; Buddle et al. 2000). Lowrie (1973) has suggested that western populations of *P. moesta* occur more often in wet habitats from various elevations. *Pardosa mackenziana* is usually associated with coniferous forests although known to inhabit salt marshes, bogs, beaches, and deciduous forests (Lowrie 1973; Dondale & Redner 1990; Buddle et al. 2000).

In a study of spider assemblages in north-central Alberta, Buddle et al. (2000) found that *P. moesta* and *P. mackenziana* co-occur in a variety of different age-classes of deciduous forest stands. The proportions of the two species, however, differed depending on whether the forest stand had a closed canopy. In open stands, 67.3% of the total catch of the two species was *P. moesta*. In closed canopy

stands the situation was reversed as 67.8% of the total catch of the two species was *P. mackenziana*.

Pardosa moesta and *P. mackenziana* are easily distinguished in the field based on their size and coloration. *Pardosa moesta* is the smaller of the two species, with an average length of 4.95 mm for males and 5.64 mm for females, whereas the average length for *P. mackenziana* is 5.91 mm for males and 6.85 mm for females (Dondale & Redner 1990). Adult and sub-adult male *P. moesta* have a dark, shiny carapace in contrast to the lighter brown carapace with its lighter median band on male and female *P. mackenziana*. Female *P. moesta* have a dark carapace with faint median and submarginal bands. It is also possible to distinguish immature stages of the two species based on subtle difference in the coloration and patterns on the carapace; immature *P. mackenziana* have distinct white setae that outline a V-pattern on the median region of the carapace. The white setae on the carapace of immature *P. moesta* are arranged in a more scattered pattern on the carapace. Additionally, the carapace of immature *P. mackenziana* is a deeper brown color than the carapace of immature *P. moesta*. Voucher specimens of both species are deposited in the Strickland Entomological Museum, University of Alberta, Edmonton, Alberta, Canada.

Density estimates.—Densities of *Pardosa* were estimated by haphazardly placing on the forest floor an upright bucket (28 cm diameter, 23 cm height) with its bottom removed. After the bucket was firmly placed on the forest floor the enclosed leaf-litter was searched for wolf spiders (similar to quadrat sampling used by Edgar (1971a, b)). Individual *Pardosa* were identified, counted and brought to the laboratory. This procedure was repeated 241 separate times between 23 April–15 June 1999. Three different life-stages were classified for both species: immatures, sub-adults, males and females. Results from the bucket estimates were extrapolated to the number of *Pardosa* of different life stages per m² of forest floor, separated into three sampling periods of approximately equal lengths (23 April–10 May, 11–27 May and 28 May–15 June).

Fecundity.—Female *P. moesta* and *P. mackenziana* carrying egg sacs, or those appearing to be gravid (i.e., found with swollen abdomens), were collected on an opportunistic

basis during the spring of 1998 and 1999 in order to assess fecundity and relationships between female size and clutch size. Many *Pardosa* species are known to produce more than one egg sac in a given season (Miyashita 1969; Edgar 1971b; Wolff 1981). However, all collections were made early in the season, ensuring that catches did not contain females with second egg sacs, which are known to contain fewer eggs (Miyashita 1969; Edgar 1971a). Data about size and fecundity were collected for a total of 66 *P. moesta* and 73 *P. mackenziana*. Live females were gently held between a piece of soft foam and a clear plastic petri dish and their carapace width (CW) was measured to the nearest 0.01 mm using an ocular micrometer. CW is easily measured and thought to be a good indicator of overall spider size, as has been shown for both web-building and hunting spiders (Hagstrum 1971; Spiller & Schoener 1990; Wise & Wagner 1992; Zimmermann & Spence 1992). Spiders were held at 25 °C under long-day photoperiod (16 h light: 8 h dark) in clear film canisters with moistened plaster-of-Paris on the bottom to maintain humidity (similar to the procedure outlined by Wise & Wagner (1992)). Many females produced egg sacs in captivity, and for most female spiders, spiderlings were allowed to hatch to determine clutch size. Due to time constraints, however, some of the specimens were placed immediately in 70% ethanol, and egg sacs were later dissected for measures of clutch size. Linear regression was used to assess the relationships between female size and number of offspring produced for each species.

Life cycle.—*Adult population dynamics:* The activity of adult wolf spiders can be assessed by using a sampling technique such as pitfall trapping. Pitfall trap catches depend on spider activity so absolute density estimates, for example, are not possible with such data. However, pitfall trap data can be used to infer the peak reproductive period for spiders as during this time male and female spider activity increases. In the present study, data generated from live-trapping and mark recapture using pitfall traps are used only to assess the activity of adult *Pardosa*, the peak reproductive period and the duration of female survival. This work was completed from May to August 1998 using enclosures previously used for experiments with ground beetles (see Nie-

melä et al. (1997)). Enclosures were located 50–60 m from the area where density estimates were obtained. Three sets of enclosures measuring 4 × 24 m in length (subdivided into six compartments per enclosure, each measuring 4 × 4 m) were made in 1989 by sinking ¾ inch (ca. 2.0 cm) plywood 30 cm into the ground, leaving 40–45 cm above ground. All seams were sealed with caulking and a strip of aluminium flashing 10 cm wide was screwed or nailed to the top part of the walls. Experiments were designed based on the assumption that *Pardosa* species would be unable to move between compartments. However, both *P. moesta* and *P. mackenziana* were observed climbing between compartments; nevertheless, it was still possible to monitor the population dynamics of adult wolf spiders within the enclosures and to assess the length of female survival.

Eight pitfall traps without preservative were placed in each of the 18 compartments. Traps were 1 liter plastic containers sunk into the ground so that the trap lip was flush with the substrate. Funnels were placed in the traps to prevent spiders from escaping. Traps were opened and monitored three to four times per week from early May until mid-July and about once per week until the end of August. I recorded the sex of captured *P. moesta* and *P. mackenziana*, and recorded whether females carried egg sacs.

Sixty *P. moesta* and 48 *P. mackenziana* females carrying egg sacs were marked and released on 16 June into the aforementioned compartments. Spiders were marked with a small dot of enamel paint on the carapace. A small hole was drilled into a petri dish that was placed over the spider being gently held on a piece of foam; females were maneuvered on the foam pad so their carapace was directly below the hole and a toothpick dipped in paint was inserted through the hole to place paint on the carapace. Marked females were monitored along with other live trap catches in the compartments in order to estimate how long individual *P. moesta* and *P. mackenziana* females survive in the field.

Juvenile growth and development: Understanding population dynamics of adult spiders is insufficient for an adequate understanding of life-cycles; additionally, it is essential to determine the growth of juvenile spiders through the course of the summer and to es-

Table 1.—Density (number per m²) of immature (IM), sub-adult (SA), male, and female *Pardosa moesta* and *P. mackenziana* obtained from 241 samples (14.94 m² total sampling area) between 23 April–15 June 1999.

Sample period	Area (m ²)	<i>Pardosa moesta</i>				<i>Pardosa mackenziana</i>			
		IM	SA	♂	♀	IM	SA	♂	♀
23 April–10 May	4.4	2.73	0.68	0	0.23	2.04	1.13	0	0
11 May–27 May	6.2	1.29	1.77	0.48	0.81	2.42	0.48	0	0.65
28 May–15 June	4.3	1.61	0	0.92	1.61	2.99	0	0.46	1.15
Average		1.87	0.81	0.47	0.88	2.48	0.54	0.15	0.60

tablish the overwintering stage. As part of an experiment investigating the competitive interactions between *P. moesta* and *P. mackenziana*, a number of newly dispersed spiderlings were released into small arenas. The arenas were white buckets, with the bottoms removed, measuring 28 cm in diameter and 23 cm in height. The buckets were sunk 5–7 cm into the ground on 8 July 1998 and covered with fine mesh to prevent immigration and emigration. Newly dispersed spiderlings were obtained from female *P. moesta* and *P. mackenziana* used for fecundity estimates. Spiderlings from more than 10 females of each species were bulk weighed in groups of ten. A total of 237 *P. moesta* and 234 *P. mackenziana* was placed in 12 arenas between 13 July–21 July 1998. In September 1998, the leaf litter from within the arenas was sifted and searched for *Pardosa* specimens. These were weighed and then immediately returned to the arenas. As soon as the snow melted in the spring of 1999, the litter within the arenas was searched a final time and *Pardosa* were counted and weighed.

Spring cohorts: To better understand what life-stages of *P. moesta* and *P. mackenziana* overwinter in central Alberta, the specimens retained from the density estimates were weighed to the nearest mg. Some additional specimens were collected on an opportunistic basis through until 30 June 1999 to increase the sample size for these estimates. It was assumed that if these species are annual, only one weight class of individuals would be present following the overwintering period. Species requiring two years to complete development should show two size classes of individuals at the time of spring emergence, and three size classes of individuals during the reproductive period (Dondale 1961; Edgar 1972).

RESULTS

Density estimates.—A total of 117 *P. moesta* and *P. mackenziana* was counted during the 241 density estimate samplings. Immature *Pardosa* represented the most frequently encountered spiders and had the highest density estimates during most sampling periods (Table 1). Densities of sub-adults were highest between 23 April–27 May and decreased in the final sampling period; adults increased in density in the last two sampling periods (Table 1). Males of both species were encountered infrequently during the survey and thus their density estimates were low in comparison to other life stages (Table 1). Female densities averaged 0.88 per m² for *P. moesta* and 0.60 per m² for *P. mackenziana*.

Fecundity.—*Pardosa moesta* was the smaller of the two species with a mean (\pm SE) CW of 2.07 ± 0.02 mm, and its average clutch size was 33.06 ± 1.29 eggs or spiderlings per egg sac. *Pardosa mackenziana* had an average CW of 2.73 ± 0.02 mm and a mean clutch size of 48.37 ± 1.67 . Both species showed a significantly positive relationship between female size and clutch size using linear regression (Fig. 1A, B). However, very little of the variation in clutch size was explained by female size as indicated by the low R² values (especially for *P. mackenziana* (Fig. 1B)).

Life cycle.—*Adult population dynamics:* Live-trapping data show that male and female *P. moesta* were most active in mid-May and early June (Fig. 2A). Peak activity of *P. mackenziana* males and females was slightly later; they were most frequently caught between late May and mid-June (Fig. 2B). Spider activity is known to vary with temperature (Dondale & Binns 1977). The high variation in live catches of adult *Pardosa* in May and June was

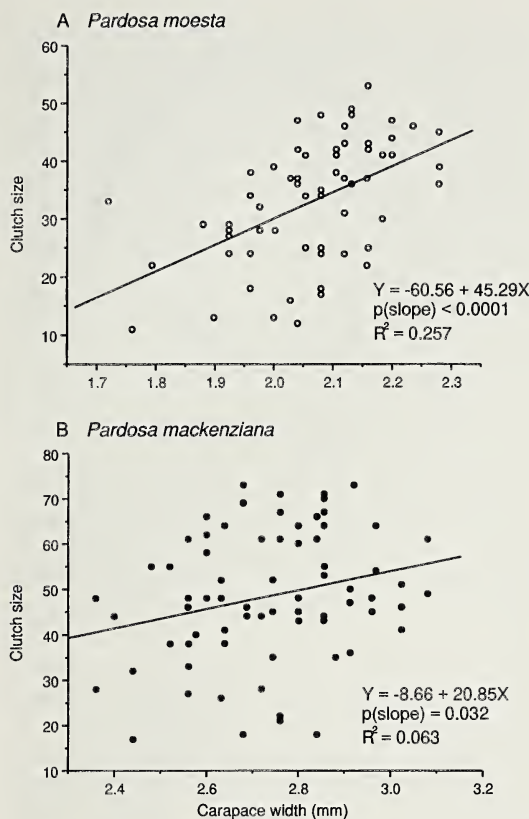


Figure 1.—Linear regression of clutch size (number of spiderlings or eggs per egg sac) against carapace width (mm) for *Pardosa moesta*, $n = 66$ (A) and *P. mackenziana*, $n = 73$ (B).

partially explained by variation in the mean daily temperatures during the spring (temperatures were obtained from a weather station at Sion, Alberta, 14 km south-west of the George Lake Field Site); warm days often corresponded to peaks in adult *Pardosa* activity (Fig. 2).

Females carrying egg sacs were caught from 31 June–25 August for *P. moesta* and from 21 May–25 August for *P. mackenziana* (Fig. 2). Therefore, spiderlings could be active from late spring and into the autumn months for both species. The late season catches of females carrying egg sacs likely corresponded to the production of a second egg sac.

Marked females were released on 16 June, and individuals of both species were re-captured at various times throughout the summer (Fig. 2). Two marked *P. moesta* were re-captured on 11 August, showing that females live at least 56 days in the field after being collected, marked and returned to the enclosures

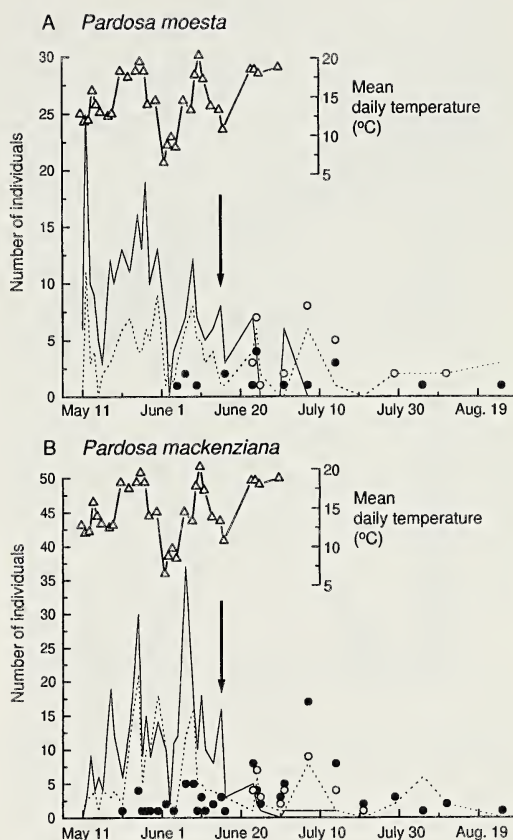


Figure 2.—Number of *Pardosa moesta* (A), and *Pardosa mackenziana* (B) collected by live trapping in enclosures between 11 May–29 August 1998. Solid lines represent catches of males, dashed lines are females. Solid circles (●) are females carrying egg sacs, open circles (○) are re-captures for marked females (released 16 June, solid arrow). Open triangles (Δ) are mean daily temperatures (°C) for May and June.

on 16 June. Female *P. mackenziana* were not found in the enclosures as long as *P. moesta*; the latest re-capture for *P. mackenziana* was 21 July, 35 days after release.

Juvenile growth and development: Spiderlings released into arenas at the beginning of this experiment (13 July–21 July) had an average weight of 0.45 ± 0.03 mg for *P. moesta* and 0.58 ± 0.04 mg for *P. mackenziana*. Weights in September were 1.30 ± 0.25 mg for *P. moesta* ($n = 29$), and 1.28 ± 0.12 mg for *P. mackenziana* ($n = 34$). Thus, *Pardosa moesta* spiderlings gained on average 2.8 times their weight, and *P. mackenziana* 2.2 times their weight between mid-July and September 1998. Leaf-litter from the arenas was

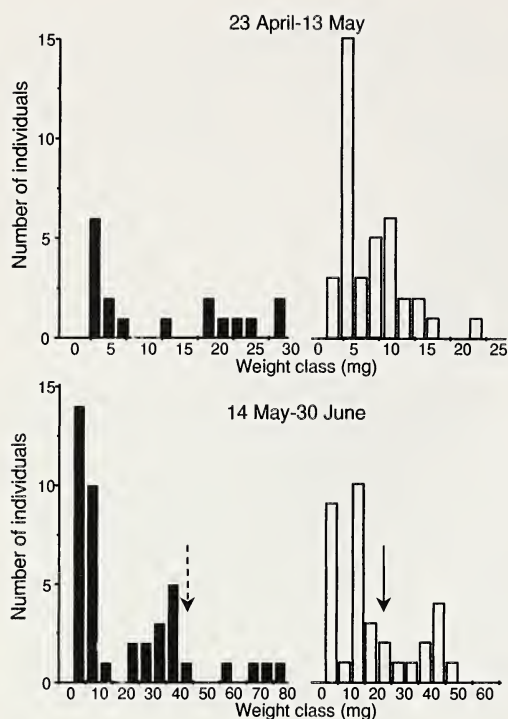


Figure 3.—Frequency of *Pardosa moesta* (open bars) and *Pardosa mackenziana* (solid bars) by weight class (mg) collected from 23 April–30 June 1999. Period of spring emergence given as 23 April–13 May, period of reproduction given as 14 May–30 June. Solid arrow indicates average weight for adult *Pardosa moesta*, dashed arrow indicates average weight for adult *Pardosa mackenziana*.

sifted and searched again on 23 April 1999; four *P. moesta* with an average weight of 1.25 ± 0.25 mg and five *P. mackenziana* with an average weight of 1.40 ± 0.25 mg overwintered in the arenas. Although the arenas only approximated natural conditions, some spiders survived the winter and did not gain weight between September 1998 and April 1999.

Spring cohorts: Spider weights from individuals retained from the density estimates indicate that two life stages, and a few larger individuals, were present immediately following winter (23 April–13 May) (Fig. 3). During the peak reproductive period (13 May–30 June), three life stages were present for both species (Fig. 3). The majority of specimens collected fell below the average weight of adult specimens (Fig. 3). Although adult *P. moesta* and *P. mackenziana* showed a peak in activity from mid-May until late June, which would correspond to the reproductive period

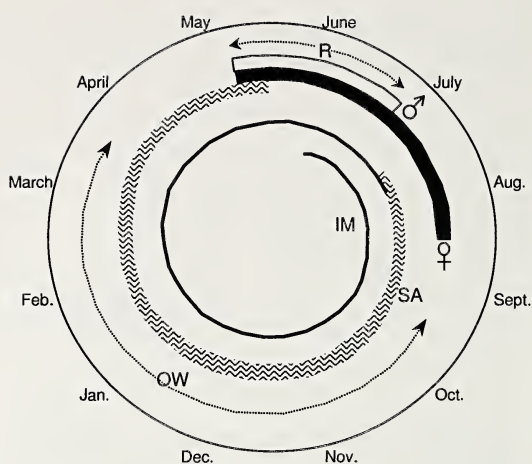


Figure 4.—Generalized life cycle of *Pardosa moesta* and *Pardosa mackenziana* in deciduous forests of central Alberta, Canada showing immatures (IM), sub-adults (SA), males, females, reproductive period (R), and overwintering period (OW).

(Fig. 2.), many smaller instars (i.e., < 5 mg in size) of both species were also present on the forest floor during this time (Fig. 3).

Taken together, results from the population dynamics of adults, juvenile growth and development, and from the weight classes of spring cohorts suggest *P. moesta* and *P. mackenziana* take two years to complete development in central Alberta. Both species have the same generalized life-cycle (Fig. 4); the only notable difference in life-cycles between the two species is that *P. moesta* has an earlier reproductive period than *P. mackenziana* (Fig. 2). Both species appear to have at least two overwintering periods: one as immatures and one as sub-adults (Fig. 4).

DISCUSSION

Density.—Densities of sub-adult and adult *P. moesta* and *P. mackenziana* were below 2.0 per m^2 during all sampling periods and immature densities were all below 3.0 per m^2 ; these estimates were lower than has been reported for other species of *Pardosa*. In Scotland, for example, Edgar (1971b) reported immature *P. lugubris* densities as high as 6.2 per m^2 for shaded areas in the spring. However, immature *P. lugubris* were also found to have low densities in clearings (Edgar 1971b); different life-stages of *Pardosa* may utilize different habitats and their densities would thus vary depending on habitat type. Immature *P.*

lugubris move from clearings to overwintering areas in the autumn, and female *P. lugubris* carrying egg sacs may search for open areas in which to sun their egg sacs and deposit their young (Edgar 1971a, b). Adult *P. moesta* are known to attain high populations in open, grassy regions (e.g., Dondale & Redner 1990; Buddle et al. 2000), which are common in the agricultural landscape within 100–200 m of the George Lake study area. Although *P. moesta* can certainly maintain populations in a closed canopy deciduous forest, densities of this species may be higher in more open habitats. Similarly, *P. mackenziana* may have higher densities in coniferous forests where this species is reported to be most commonly collected (Dondale & Render 1990).

Although densities of immature *P. moesta* and *P. mackenziana* remained between 1.29–2.99 per m² during all three sampling periods at George Lake, sub-adult and adult densities varied more dramatically by sampling period. Sub-adult densities of both species decreased as spring progressed as sub-adults molted to sexually mature adults during the peak reproductive period from mid-May to late June. Male densities were low for both species, which may reflect their higher mobility; males may have been better able to escape when the bucket was placed on the forest floor.

Fecundity.—Measures of both female spider size and fecundity varied considerably in *P. moesta* and *P. mackenziana*. Overall, however, both species were substantially larger than the average for Canada. *Pardosa moesta* has previously been reported as having an average CW (± 1 SD) of 1.91 ± 0.14 mm ($n = 20$) and the average CW for *P. mackenziana* has been reported as 2.55 ± 0.17 mm ($n = 136$) (Lowrie & Dondale 1981; Dondale & Redner 1990). The clutch size of 48.37 for *P. mackenziana* is close to the estimate of 50 reported by Lowrie & Dondale (1981) but was substantially lower than the estimate of 57.5 provided by Schmoller (1970) for alpine populations in Colorado.

In general, the average female size of a spider species is positively correlated with average clutch size (Marshall & Gittleman 1994). Using data from Schmoller (1970), Lowrie & Dondale (1981), Marshall & Gittleman (1994), and unpublished data for *P. xerampelina*, I used linear regression to assess the strength of this relationship for *Pardosa*

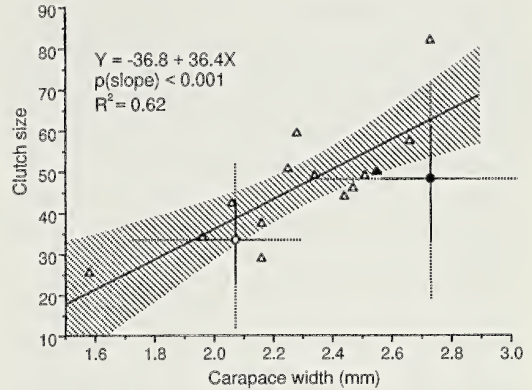


Figure 5.—Linear regression of clutch size against carapace width (mm) for 14 species of *Pardosa* (Δ) using data from Schmoller (1970), Lowrie & Dondale (1981), Marshall & Gittleman (1994) and C. Buddle (unpubl. data). Shaded area represents the 95% confidence limits for the regression line. Solid triangle (▲) represents a published estimate for *Pardosa mackenziana* (from Lowrie & Dondale (1981)). Estimates for *Pardosa moesta* (○) and *Pardosa mackenziana* (●) from George Lake are averages with one standard deviation (solid horizontal and vertical lines) and range (dashed horizontal and vertical lines) for both carapace width and clutch size.

species. Using data for 14 species of *Pardosa*, there is a positive relationship between species size and clutch size, and close to two-thirds of the variation in clutch size is explained by species size ($R^2 = 0.62$, Fig. 5). Clutch size for *P. moesta* at George Lake is close to what can be expected based on its size alone. However, the estimates for *P. mackenziana* from George Lake fell farther below what was expected, and out of the 95% confidence limits for the regression line (Fig. 5). Thus, understanding variation in fecundity demands more than simply an understanding of size.

Within a species, however, there are strong relationships between female size and fecundity for both web-building and hunting spiders (e.g., Wise 1979, 1993; Enders 1976; Beck & Conner 1992; Simpson 1995). Although positive relationships characterized both *P. moesta* and *P. mackenziana*, female size is clearly not the only determinant of fecundity. Kessler (1971) showed that food shortages can affect the number of eggs in two species of *Pardosa*. Furthermore, in a study of food limitation on the reproductive output of the pisaurid *Dolo-*

medes triton Walckenaer 1837, Spence et al. (1996) also showed that food limitation may be important in determining clutch size, but that these effects may vary with female size. Clutch size is dependent on the individual condition of the female; and this will vary depending on various factors such as environmental conditions, prey availability, and habitat type.

Life cycle.—The population dynamics of adult *P. moesta* and *P. mackenziana* were inferred from live pitfall trapping, a technique that depends on the activity of individual spiders. Focussing on these data, it appears that *P. moesta* and *P. mackenziana* follow a pattern typical for life histories of *Pardosa* in temperate zones: sub-adults must overwinter since mating occurs early in the spring, males die shortly after the reproductive period, and females carry egg sacs into the summer months (Turnbull 1966; Edgar 1971a). There were only two notable differences in adult activity between the two species: female *P. moesta* may live longer than *P. mackenziana*, and the reproductive period for *P. moesta* is slightly earlier than for *P. mackenziana*, a finding also noted by Wolff (1981).

By itself, the phenological data for adult populations could be interpreted to mean that both species have annual life-cycles. However, data about juvenile growth and development and weight classes of spring cohorts establish that more than one year is required for these species to mature. The numerous small (i.e., < 5 mg) individuals of *P. moesta* and *P. mackenziana* found in the early spring would require at least one more year to complete their development. Also, *P. moesta* and *P. mackenziana* spiderlings held in outdoor arenas did not reach the sub-adult stage in their first growing season and would require an additional overwintering period to complete their development.

During the period of spring emergence, weights of immature *Pardosa* specimens did not fall into a single weight class but were spread over several weight classes (Fig. 3). This may reflect the different cohorts produced from early (i.e., mid-May until June) compared to mid-season (i.e., late June until July) egg sacs from the previous summer. Spiderlings dispersing from mid-season egg sacs would not have the same potential for growth and development before the onset of cooler

conditions compared to spiderlings dispersing from early season egg sacs. This suggests that overwintering for immature *P. moesta* and *P. mackenziana* may be facultative rather than obligatory; immature spiderlings may overwinter at different stages in their development. However, the reproductive period for both species is early in the spring, suggesting that the second overwintering stage primarily consists of sub-adults.

To ensure synchrony of the mating period, spiderlings from mid-season egg sacs would have to gain proportionally more size during their second summer compared to those from early season egg sacs. *Pardosa* may accomplish this by altering the number of instars to reach maturity, as instar number is flexible in many spider species (e.g., Miyashita 1968; Edgar 1972; Toft 1976; Zimmermann & Spence 1998). Edgar (1971a) also showed that although the second egg sacs of *P. lugubris* had fewer eggs, the eggs themselves were heavier, possibly in preparation for cooler winter conditions.

A small number of female *P. moesta* and *P. mackenziana* carry egg sacs much later in the season than the majority of the populations (i.e., late August, Fig. 2). Since spiderlings emerging from these egg sacs would be substantially smaller than those emerging earlier in the season, it is possible that spiderlings from late season egg sacs may slow down their development and stretch their life cycle over two additional growing seasons. By implementing a three year life cycle, synchrony of mating would be ensured. However, because only a small proportion of female *P. moesta* and *P. mackenziana* carry egg sacs in late August, it is unlikely that many individuals in the central Alberta populations of these species would exhibit three year life-cycles. Most egg sacs are carried in early or mid-season, suggesting the majority of individuals of *P. moesta* and *P. mackenziana* have biennial life cycles.

A two year life cycle for *P. moesta* and *P. mackenziana* is similar to that found for *P. lugubris* in central Scotland (Edgar 1971b), and for several species living at high altitudes (Schmoller 1970). Further south it is probable that *P. moesta* and *P. mackenziana* have annual life cycles. Schmoller (1970), for example, suggested that in high altitude regions of Colorado, *P. mackenziana* exhibits annual life

cycles. *Pardosa lugubris* has an annual life-cycle on the European mainland (Vlijm et al. 1963), and a biennial life-cycle in central Scotland (Edgar 1971b). The difference in life-cycle is attributed to cooler conditions in Scotland. However, Edgar (1972) also showed that the life cycle of *P. lugubris* in the Netherlands may vary from annual to biennial depending on environmental conditions and the timing of spiderling dispersal. A mixed annual-biennial life cycle has also been suggested for *P. tesquorum* (Odenwall 1901) in central Saskatchewan (D.J. Buckle unpubl. data). Another variation in *Pardosa* life-cycles has been shown for *P. agrestis* (Westring 1861) in central Europe. Here, Samu et al. (1998) report a bimodal life-history pattern, with reproductive periods in May and August. Undoubtedly, *Pardosa* life-cycles are remarkably flexible, and this may aid in explaining their dominance in many terrestrial ecosystems.

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A STRUCTURED INVENTORY OF APPALACHIAN GRASS BALD AND HEATH BALD SPIDER ASSEMBLAGES AND A TEST OF SPECIES RICHNESS ESTIMATOR PERFORMANCE

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ABSTRACT. The current rate of species attrition necessitates the development of quick and accurate sampling protocols and species richness estimators. Four time-based and one area-based methods were used to sample spiders of a grass bald and a heath bald in the Great Smoky Mountains National Park in late spring and early fall of 1995. Eighty-four samples were collected at each site; 1853 adults and 91 species were found in the grass bald, 573 adults and 60 species in the heath bald. The data were analyzed with 11 species richness estimators: Chao & Lee 1, Chao & Lee 2, ACE, ICE, bootstrap, Chao 1, Chao 2, first-order jackknife, second-order jackknife, Michaelis-Menten runs, and Michaelis-Menten means. All but the Chao & Lee estimators generated richness estimates that clustered within a reasonable range, 106–160 species for the grass bald and 68–90 species for the heath bald. The failure of the observed species accumulation curve to level off for our data sets showed that more sampling would be needed to determine the number of species present as adults during the two sampling seasons. Although this prevented us from rigorously testing richness estimator performance, we found that the Michaelis-Menten means estimator performed better than the other estimators when judged by two indirect criteria of good estimator performance—the estimator curve should reach an asymptote with fewer samples than are required for the observed species accumulation curve to reach an asymptote, and the estimates should be close to reasonable visual extrapolations of the asymptote of the observed species accumulation curve. We postulate that the differences we found in species richness and taxon and guild composition between the spider assemblages of these two bald communities are, at least in part, a consequence of striking differences in the physiognomy, richness, and taxonomic composition of the plant associations of the two communities.

Keywords: Spiders, species richness, richness estimators, Appalachian balds

In order to know how and where to protect biodiversity, it is imperative that we learn more about the patterns of diversity of terrestrial arthropods, which may comprise 80% or more of the Earth's species but have too often been neglected by resource managers and conservation planners (Wilson 1988, 1992; Kremen et al. 1993; Colwell & Coddington 1994; Longino 1994). Spiders, which include about 36,000 described species and are estimated to number 60,000–170,000 species (Coddington & Levi 1991; Platnick 1999), comprise a significant portion of this terrestrial arthropod diversity. Spiders are abundant and ubiquitous,

employ a remarkable diversity of predation strategies, occupy a wide array of spatial and temporal niches, are characterized by high within-habitat taxonomic diversity, exhibit taxon- and guild-specific responses to environmental change, and are relatively easy to sample and identify. They are important regulators of insect populations (Riechert & Lockley 1984; Riechert & Bishop 1990; Wise 1993) and may prove to be useful indicators of the overall species richness and health of biotic communities (Kremen et al. 1993; Colwell & Coddington 1994; Norris 1999).

Coddington et al. (1991) pioneered the development of a sampling protocol and estimation procedure for rapid assessment of spider diversity at tropical forest sites. This and similar protocols can be structured to provide replicated data sets that reflect the relative abundance of species in the sites and habitats studied and may therefore provide comparable views of species richness, taxonomic compo-

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sition, and guild structure across diverse communities and regions (Coddington et al. 1996; Silva & Coddington 1996; Dobyns 1997). Colwell & Coddington (1994) reviewed and explored the performance of richness estimators and emphasized the need to test these with real data sets.

Balds, natural tree-less communities located on well-drained high-elevation sites below the climatic tree-line, are among "the most distinctive and celebrated" communities of the southern Appalachian Mountains (Whittaker 1956; Mark 1958). Despite considerable research, there is no clear understanding of the factors responsible for the origin and maintenance of these communities (Cain 1930; Whittaker 1956; Billings & Mark 1957; Mark 1958; Stratton & White 1982). Grass balds, because of their high plant species richness, aesthetic appeal, and shrinking size (due to forest encroachment), are currently the focus of special monitoring and management efforts by resource specialists in the Great Smoky Mountains National Park (GSMNP) (Keith Langdon pers. com.). Heath balds, which are dense thickets of evergreen ericaceous shrubs on highly acidic soil, support far fewer plant species and a more homogeneous architecture than grass balds, but attract considerable attention because of their colorful floral displays.

In the current study we employ a modified Coddington protocol and eleven richness estimator algorithms and other analytical methods to provide the first estimates of the species richness and structure of spider assemblages in a grass bald and a heath bald. Additionally, we use these data sets to evaluate the performance of the richness estimators.

METHODS

Study sites.—The two sites are 40 km apart in the GSMNP. Gregory Bald, the grass bald site, covers a very gently rounded peak (UTM grid coordinates: E2400, N39343) and ranges from 1490–1510 m elevation. This bald covers about 3 hectares and contains 175 vascular plant species, more than any other bald in the GSMNP (Stratton & White 1982). It consists of large open grassy areas interrupted by patches of shrubs (up to 2 m tall) and, occasionally near its edge, small trees (up to 15 m tall). The dominant grasses are mountain oats (*Danthonia* spp.) and blue grasses (*Poa* spp.);

the dominant shrubs are blueberries (*Vaccinium* spp.), hawthorns (*Crataegus* spp.) and azaleas (*Rhododendron* spp.). The ground surface is covered by thin mats of dead grasses and sedges in grassy areas and a thin layer of leaf litter below the shrubs.

The heath bald site (UTM grid coordinates: E2788, N39460) covers 0.5 hectares at 1380–1410 m elevation on the southeast-facing slope both above and below a 50 m stretch of Alum Cave Trail immediately below Inspiration Point (which is on a ridge extending south from Peregrine Peak). Cain (1930) found that nearby heath balds supported only 12 plant species. The heath bald at this site is a homogeneous, dense, woody mass of interwoven ericaceous shrubs about 3–4 m tall; rhododendron (*Rhododendron catawbiense*) and mountain laurel (*Kalmia latifolia*) dominate; *Vaccinium*, Carolina rhododendron (*R. minus*), greenbriar (*Smilax*), and sand myrtle (*Leiophyllum buxifolium*) are also present. The ground, virtually devoid of herbaceous plants, is covered by a thick layer of leaf litter (interrupted in places by patches of short compact moss) over thick, moist, spongy humus.

Data collection.—Our sampling procedure included five methods chosen to access all microhabitats in these two communities: aerial hand collection, ground hand collection, beating, Tullgren funnel litter extraction, and sweep-netting. The first four methods were used in the heath bald; sweep-netting was substituted for aerial hand collection in the grass bald due to the predominance of low vegetation in that community. The aerial and ground hand collection methods are synonymous with the "looking up" and "looking down" methods, respectively, of Coddington et al. (1991). Aerial sampling involves searching leaves, branches, tree trunks, and spaces in between, from knee height up to maximum overhead arm's reach. Ground collection involves searching on hands and knees, exploring the leaf litter, logs, rocks, and plants that are below knee level. Beating consists of striking vegetation at any level with a 1 m long stick and catching the falling spiders on a tray held horizontally below the vegetation. Because the dense maze of shrub branches throughout the heath bald and in some parts of the grass bald made it difficult to maneuver the standard 0.5 m² beating sheet, we used instead a smaller (0.24 m²), rigid, rectangular (57 × 42 cm)

plastic tray with a 1.5 cm high rim. The opening of the heavy sweep net used for sweep-netting was 0.37 m in diameter; at 225–425 sweeps per hour (mean = 327.5) and a mean sweep length of 1.4 m, an average of 49 m³ of habitat volume was sampled per hour. For all of these methods, fingers, glass vials, and aspirators were used to collect spiders into 80% ethanol. Each litter sample consisted of 1 m² of leaf litter and underlying loose humus that was placed in a plastic bag, transported to the lab, and processed in 50–60 cm diameter Tullgren funnels fitted with 6–8 mm mesh screens and 60 watt light bulbs for two–four days until the litter was dry. In grassy areas of the grass bald, where much of the litter was interlocked with grass and low herbs, a long knife was used to cut away and collect thin sections of sod.

Except for the litter samples, time was used to partition sampling effort into replicate samples; one sample unit equals one hour of uninterrupted time during which a collector attempts to collect every spider encountered that is not obviously a juvenile. During any one sampling hour each of the three collectors (the authors) used only one method, but the team as a whole employed all three time-based methods in the same portion of the site. Sampling effort was distributed so that, in each sampling season, no area within the site was sampled more than once with a given method and nearly all of the available habitat area was sampled. Because of the density and height of the heath vegetation, the area sampled per hour was much smaller in the heath bald than in the grass bald. It should be noted that since sweeping was substituted for aerial hand sampling on the grass bald and since it took more time and effort to maneuver in the heath (which biases time-based samples), considerable caution must be exercised when making between-community comparisons of the abundance or relative abundance of taxa. In particular, these differences may bias Kulczynski's index of similarity (see below). Night sampling was tried (3 one-hour samples in the grass bald), but, since the rate of capture of adults was so low (2.3 per hour), sampling was limited to daylight hours. Sampling was conducted in the spring and fall of 1995: 25–26 May and 23–24 September in the heath bald; 3–5 June and 29 September–1 October in the grass bald. Forty-two samples (36 one-

hour samples distributed equally among the three time-based methods and six litter samples) were collected at each site in each season. Although many juveniles end up in each sample, only adults were counted, identified, and used in analyses because identifying juveniles to species is often impossible. The specimens, which are being curated temporarily at Western Carolina University, will eventually be deposited in the National Museum of Natural History of the Smithsonian Institution.

Data analysis.—The computer program EstimateS (Version 5.0.1) (Colwell 1997) was used to evaluate the performance of the following 11 species richness estimators with our data sets: Chao & Lee 1, Chao & Lee 2, ACE, ICE, Chao 1, Chao 2, first-order jackknife, second-order jackknife, bootstrap, Michaelis-Menten runs, and Michaelis-Menten means. The two Michaelis-Menten estimators use the same equation, a two-parameter hyperbolic function first used to describe enzyme kinetics, to directly extrapolate the species accumulation curve, but they differ in computational format (Colwell & Coddington 1994; Colwell 1997). The other nine estimators are non-parametric algorithms which estimate the number of species yet-to-be-collected based on a quantification of rarity. Chao & Lee 1, Chao & Lee 2, ACE, and ICE are coverage-based richness estimators based on the statistical concept of sample coverage. ACE (abundance-based coverage estimator) (Chao et al. 1993) and ICE (incidence-based coverage estimator) (Lee & Chao 1994) are modified versions of the two Chao & Lee (1992) estimators, which have been found to consistently overestimate richness, especially with small samples (Colwell & Coddington 1994; Colwell 1997). Chao & Lee 1, Chao & Lee 2, ACE, and Chao 1 are all abundance-based estimators; that is, they use abundance to quantify rarity (for example, the number of singletons and doubletons, which are the number of species represented by only one or two individuals in the entire data set). ICE, Chao 2, both jackknife estimators, and the bootstrap estimator are incidence-based; they rely on incidence (presence/absence) data to quantify rarity (for example, the number of uniques and duplicates, which are the number of species found in only one or two samples in the entire data set). We used the Coleman curve,

which plots the expected richness for random subsamples of the entire data set, to determine whether the samples are uniform enough to justify use of the Michaelis-Menten estimators (Colwell & Coddington 1994; Colwell 1997).

See Colwell & Coddington (1994), Colwell (1997), and Chazdon et al. (1998) for descriptions and discussions of these estimator algorithms and for a demonstration of how EstimateS tracks changes in each richness estimate as samples accumulate. From a species-by-sample abundance matrix, the program selects a sample, calculates the richness estimates based on that sample, selects a second sample, recomputes the estimates using the data from both samples, and so on until all samples are included. By randomizing sample order (we chose 100 randomizations) and computing the mean richness estimate for each sample accumulation level, the program removes the effect of sample order and generates a smoother species accumulation curve, thereby permitting closer comparison of estimator performance. The fact that the Coleman estimator curve was nearly identical to the species accumulation curve in all of our data sets indicates that our samples are not especially heterogeneous, and that randomization of sample accumulation order is therefore justified (Colwell & Coddington 1994). Using the same randomization protocol, we also plotted the mean number of singletons, uniques, doubletons, and duplicates against sample number.

Percentage complementarity (Colwell & Coddington 1994), Kulczynski's index of similarity (also called the Bray-Curtis index) (Bray & Curtis 1957), and Sorensen's index of similarity (Kent & Coker 1992) were used to compare the taxonomic composition of the two bald communities. Percentage complementarity = $100(x/y)$, where x = number of unique species (collected in only one community or the other), and y = total number of species collected in both communities (combined species richness). Kulczynski's index of similarity (K) = $2w/(a + b)$, where a = number of individuals collected in community A, b = number of individuals collected in community B, and w = sum of the lesser abundances for those species present in both communities. Sorensen's index of similarity (S) = $2e/(c + d)$, where c = number of species collected in community A, d = number of spe-

cies collected in community B, and e = number of species common to both communities. Percentage complementarity is a measure of difference. Kulczynski's index is a measure of similarity and, because it uses abundance data, emphasizes the importance of common species. Sorensen's index, also a measure of similarity, does not emphasize the importance of common species.

RESULTS

A total of 2426 adult spiders representing 22 families, 89 genera, and 128 species was present in the 168 samples collected in this study (see Table 1 for breakdowns by community and season). The number of adults collected and the observed richness were much higher in the grass bald than in the heath and were higher in the spring than in the fall in both communities (Table 2). Sampling intensity, the ratio of adults to species, was higher for the grass bald than for the heath bald (Table 2). The inventory completeness index (the percentage of species that is not singletons), another indication of how well a community has been sampled, was slightly lower for the grass bald than for the heath bald (Table 2).

Species richness estimates.—For none of the six sample sets (the total sample for each community and the two seasonal subsets for each community) does the mean, randomized, observed species accumulation curve reach an asymptote (Figs. 1–6), although these curves for the three heath community data sets (Figs. 2, 5, 6) appear to more closely approach an asymptote than do those of the corresponding grass bald data sets (Figs. 1, 3, 4). The Michaelis-Menten, ICE, and Chao 2 estimator curves approach an asymptote more rapidly as sample number increases than do the other estimator curves (Figs. 1–6). In all six data sets, the Michaelis-Menten estimate appears to approach an asymptote more closely than do the other estimates. The second-order jackknife estimates climb more steeply for every data set than do the first-order jackknife estimates. The shape of the bootstrap estimator curve departs relatively little from the observed species accumulation curve. As predicted by Colwell (1997), the Michaelis-Menten runs estimator generated especially high and erratic richness estimates early in the curve. Since this estimator leveled off to nearly the same values as the Michaelis-Menten means, only

Table 1.—Species collected in bald communities; numbers of adults given for spring and fall sample sets (42 samples per set). Classification follows Platnick (1997), except that linyphiids are divided into subfamilies. Guild designations (based on our collecting data and literature): AW = aerial web-builder, AH = aerial hunter, GW = ground web-builder (web in, or attached to, ground litter), GH = ground hunter; AG and GA mean, respectively, primarily aerial or primarily ground. Erigonine linyphiids and leptonetids were assigned to web-building guilds even though for many of these species it is not known whether webs are used in prey capture. Singleton status designations (based on identified GSMNP collections): C = common in GSMNP (in one or more other habitats), U = apparently uncommon in GSMNP.

Taxon	Grass bald		Heath bald		Guild	Single- ton status
	Spring	Fall	Spring	Fall		
Agelenidae						
<i>Agelenopsis utahana</i> (Chamb. & Ivie)	0	3	0	4	AW	
Amaurobiidae						
<i>Callobius bennetti</i> (Blackw.)	0	0	0	1	AW	C
<i>Cybaeopsis armipotens</i> (Bishop & Crosby)	4	0	0	0	GW	
<i>Cybaeopsis pantoplus</i> (Bishop & Crosby)	0	0	1	14	GW	
<i>Coras montanus</i> (Emerton)	0	0	1	2	GW	
<i>Wadotes calcaratus</i> (Keys.)	0	3	0	0	GW	
<i>Wadotes hybridus</i> (Emerton)	0	1	0	0	GW	C
<i>Wadotes tennesseensis</i> Gertsch	0	0	3	6	GW	
Antrodiaetidae						
<i>Antrodiaetus unicolor</i> (Hentz)	0	8	12	9	GW	
Anyphaenidae						
<i>Wulfilia saltabunda</i> (Hentz)	0	1	0	0	AH	U
Araneidae						
<i>Araneus trifolium</i> (Hentz)	0	12	0	0	AW	
<i>Araniella displicata</i> (Hentz)	2	0	0	0	AW	
<i>Argiope aurantia</i> Lucas	0	2	0	0	AW	
<i>Argiope trifasciata</i> (Forsk.)	0	1	0	0	AW	C
<i>Eustala cepina</i> (Walck.)	0	0	1	0	AW	U
<i>Gea heptagon</i> (Hentz)	0	3	0	0	AW	
<i>Hyposinga rubens</i> (Hentz)	13	0	0	0	AW	
<i>Neoscona arabesca</i> (Walck.)	0	3	0	0	AW	
<i>Neoscona hentzi</i> (Keys.)	0	3	0	0	AW	
Clubionidae						
<i>Clubiona canadensis</i> Emerton	4	0	3	0	AH	
<i>Clubiona kastoni</i> Gertsch	1	0	0	0	AH	C
<i>Clubiona rhododendri</i> Barrows	66	34	2	3	AGH	
<i>Clubiona spiralis</i> Emerton	0	0	7	10	GAH	
<i>Clubiona</i> sp. A	1	0	0	0	AH	U
Cybaeidae						
<i>Cybaeus patritus</i> Bishop & Crosby	0	0	0	4	GW	
Dictynidae						
<i>Cicurina breviararia</i> Bishop & Crosby	1	2	1	2	GW	
<i>Cicurina brevis</i> Emerton	0	0	1	0	GW	C
<i>Cicurina minima</i> Chamb. & Ivie	0	0	6	10	GW	
<i>Dictyna maxima</i> (Banks)	0	0	1	0	AW	U
<i>Lathys immaculata</i> Chamb. & Ivie	1	0	1	12	GW	C
Gnaphosidae						
<i>Zelotes hentzi</i> Barrows	4	0	0	0	GH	

Table 1.—Continued.

Taxon	Grass bald		Heath bald		Guild	Single- ton status
	Spring	Fall	Spring	Fall		
Hahniidae						
<i>Calymmaria persica</i> (Hentz)	0	0	2	6	GW	
<i>Cryphoea montana</i> Emerton	0	0	6	1	GW	
<i>Neoantistea agilis</i> (Keys.)	1	7	0	0	GW	
<i>Neoantistea magna</i> (Keys.)	2	11	5	15	GW	
Leptonetidae						
<i>Appaleptoneta coma</i> (Barrows)	0	0	0	1	GW	C
<i>Appaleptoneta silvicultrix</i> (Crosby & Bishop)	0	0	0	2	GW	
Linyphiidae						
Erigoninae						
<i>Blestia sarcocuon</i> (Crosby & Bishop)	4	36	2	3	GW	
<i>Ceraticelus alticeps</i> Fox	564	434	3	6	AW	
<i>Ceraticelus carinatus</i> Emerton	12	77	6	14	GW	
<i>Ceratinella brunea</i> Emerton	2	3	0	0	GW	
<i>Ceratinops carolinus</i> Banks	1	0	1	0	GW	C
<i>Ceratinopsidis formosa</i> Banks	0	0	0	1	AW	C
<i>Collinsia oxypaederotipus</i> (Crosby)	128	2	85	0	GW	
<i>Eperigone trilobata</i> (Emerton)	1	0	0	0	GW	U
<i>Eridantes erigonoides</i> Emerton	8	0	0	0	GW	
<i>Erigone autumnalis</i> Emerton	11	2	0	0	GW	
<i>Erigone brevidentata</i> Emerton	4	0	0	0	GW	
<i>Floricomus praedesignatus</i> Bishop & Crosby	10	1	11	11	GW	
<i>Gonatium crassipalpum</i> Bryant	0	3	0	0	AW	
<i>Grammonota pictilis</i> (O.P.-Cambr.)	0	0	2	0	AW	
<i>Maso sundevallii</i> (Westring)	6	0	0	0	GW	
<i>Pelecopsis moesta</i> (Banks)	12	12	0	0	GW	
<i>Pocadicnemus americana</i> Milledge	3	0	17	0	GAW	
<i>Scylaceus pallidus</i> (Emerton)	0	7	0	0	GW	
<i>Walckenaeria digitata</i> (Emerton)	4	0	0	0	GAW	
<i>Walckenaeria directa</i> (O.P.-Cambr.)	1	1	3	5	GW	
<i>Walckenaeria minuta</i> (Emerton)	0	0	3	1	GW	
<i>Walckenaeria pallida</i> (Emerton)	0	0	1	0	GW	C
<i>Walckenaeria spiralis</i> (Emerton)	4	0	0	0	GW	
Erigoninae sp. A	0	0	0	1	GW	U
Erigoninae sp. B	0	2	0	0	AW	
Erigoninae sp. C	0	1	0	0	AW	U
Linyphiinae						
<i>Bathyphantes bishopi</i> Ivie	4	50	16	2	GW	
<i>Bathyphantes pallidus</i> (Banks)	0	1	0	0	GW	U
<i>Centromerus denticulatus</i> (Emerton)	0	0	0	1	GW	C
<i>Florinda coccinea</i> (Hentz)	39	7	0	0	AW	
<i>Frontinella pyramitela</i> (Walck.)	0	0	0	1	AW	C
<i>Lepthyphantes zebra</i> (Emerton)	17	0	56	29	GW	
<i>Meioneta micaria</i> (Emerton)	8	1	2	0	GAW	
<i>Meioneta semipallida</i> Chamb. & Ivie	0	5	0	0	GAW	
<i>Neriene radiata</i> (Walck.)	0	0	9	0	AW	
<i>Neriene redacta</i> Chamb.	0	5	0	0	GAW	
<i>Neriene variabilis</i> (Banks)	0	0	0	1	GAW	C
<i>Tapinopa bilineata</i> Banks	0	0	0	1	GW	U
<i>Taranucnus ornithes</i> (Barrows)	0	0	1	1	GW	

Table 1.—Continued.

Taxon	Grass bald		Heath bald		Guild	Single- ton status
	Spring	Fall	Spring	Fall		
Liocranidae						
<i>Phrurotimpus borealis</i> (Emerton)	3	0	18	0	GH	
<i>Scotinella</i> sp. A	0	0	2	0	GH	
Lycosidae						
<i>Allocosa funerea</i> (Hentz)	0	1	0	0	GH	U
<i>Arctosa virgo</i> (Chamb.)	3	0	0	0	GH	
<i>Pardosa atlantica</i> Emerton	1	0	0	0	GH	U
<i>Pardosa milvina</i> (Hentz)	1	0	0	0	GH	C
<i>Pardosa saxatilis</i> (Hentz)	1	0	0	0	GH	C
<i>Pirata hiteorum</i> Wallace & Exline	0	6	0	0	GH	
<i>Pirata montanus</i> Emerton	1	2	0	0	GH	
<i>Schizocosa bilineata</i> (Emerton)	1	0	0	0	GH	U
<i>Varacosa avara</i> (Keys.)	1	0	0	0	GH	C
Nesticidae						
<i>Nesticus reclusus</i> Gertsch	0	0	2	2	GW	
Oxyopidae						
<i>Oxyopes salticus</i> Hentz	5	0	0	0	AH	
Philodromidae						
<i>Philodromus montanus</i> Bryant	2	0	0	0	AH	
Salticidae						
<i>Eris marginata</i> (Walck.)	0	0	0	2	AH	
<i>Evarcha falcata</i> (Clerck)	5	3	0	0	AH	
<i>Ghelnia canadensis</i> (Banks)	5	4	0	0	GH	
<i>Habrocestum pulex</i> (Hentz)	1	0	2	0	AH	C
<i>Habronattus coecatus</i> (Hentz)	1	0	0	0	AH	C
<i>Hentzia mitrata</i> (Hentz)	2	0	0	0	AH	
<i>Maevia inclemens</i> (Walck.)	12	0	0	0	AH	
<i>Maevia</i> sp. A	2	1	14	4	AH	
<i>Neon nellii</i> Peckham & Peckham	17	3	21	0	GH	
<i>Pelegrina montana</i> (Emerton)	1	0	0	0	GH	C
<i>Pelegrina proterva</i> (Walck.)	18	8	0	1	AGH	C
<i>Pelegrina</i> sp. A	1	0	0	0	AH	U
<i>Phidippus clarus</i> Keys.	0	3	0	0	AH	
<i>Phidippus mystaceus</i> (Hentz)	0	1	0	0	AH	U
<i>Talavera minuta</i> (Banks)	1	0	0	0	GH	U
<i>Thiodina puerpera</i> (Hentz)	1	0	0	0	AH	C
<i>Zygoballus bettini</i> Peckham	2	0	0	0	AH	
<i>Zygoballus sexpunctatus</i> (Hentz)	1	0	0	0	AH	C
Tetragnathidae						
<i>Tetragnatha laboriosa</i> Hentz	5	0	0	0	AW	
<i>Zygiella dispar</i> (Kulczynski)	0	0	0	2	AW	
Theridiidae						
<i>Dipoena nigra</i> (Emerton)	1	0	0	0	AW	C
<i>Pholcomma barnesi</i> Levi	0	0	1	0	GW	U
<i>Pholcomma hirsutum</i> Emerton	0	0	1	1	GW	
<i>Robertus frontatus</i> (Banks)	1	0	0	0	GW	C
<i>Theridion differens</i> Emerton	0	0	2	0	AW	
<i>Theridion frondeum</i> Hentz	0	1	0	0	AW	C
<i>Theridion intervallatum</i> Emerton	0	1	0	0	AW	U

Table 1.—Continued.

Taxon	Grass bald		Heath bald		Guild	Single- ton status
	Spring	Fall	Spring	Fall		
<i>Theridion lyricum</i> Walck.	0	0	7	0	AW	U
<i>Theridion neshamini</i> Levi	1	0	0	0	AW	
<i>Theridion sexpunctatum</i> Emerton	0	0	30	0	AW	
<i>Theridula opulenta</i> (Walck.)	23	2	0	0	AW	
Theridiosomatidae						
<i>Theridiosoma gemmosum</i> (L. Koch)	0	0	7	0	GW	
Thomisidae						
<i>Misumena vatia</i> (Clerck)	0	0	1	0	AH	U
<i>Misumenoides formosipes</i> (Walck.)	0	1	0	0	AH	C
<i>Misumenops asperatus</i> (Hentz)	3	0	0	0	AH	
<i>Misumenops oblongus</i> (Keys.)	5	0	0	0	AH	
<i>Ozyptila distans</i> Dondale & Redner	0	0	0	3	GH	
<i>Xysticus triguttatus</i> Keys.	1	0	0	0	GH	U
Total	1072	781	378	195		

Table 2.—Richness estimates and other summary values for each bald community and for each seasonal sample set from each community. Each richness estimate represents the mean (and, for some estimators, the SD) for 100 randomizations of sample order. Sampling intensity is the ratio of individuals to species. Inventory completeness is the percentage of species that are not singletons. Adjusted estimate range is the range of all but the Chao & Lee richness estimate values divided by the observed number of species.

	Grass bald			Heath bald		
	All samples	Spring samples	Fall samples	All samples	Spring samples	Fall samples
Richness estimates						
Chao & Lee 1	948.1	558.3	262.7	106.5	90.4	59.5
Chao & Lee 2	9147.8	4307.1	1260.1	150.9	144.1	73.0
ACE	120.9	93.6	59.4	75.6	57.5	53.6
ICE	125.3	99.8	65.0	76.8	57.9	52.5
Chao 1	159.6 ± 36.7	110.6 ± 25.5	62.0 ± 9.9	72.8 ± 8.4	54.4 ± 6.8	51.1 ± 8.8
Chao 2	139.2 ± 22.7	101.6 ± 18.2	71.1 ± 14.8	82.6 ± 13.9	61.6 ± 11.0	53.1 ± 9.6
first-order jackknife	124.6 ± 6.0	93.3 ± 5.9	65.6 ± 4.2	78.8 ± 4.5	59.6 ± 3.7	53.6 ± 3.9
second-order jack- knife	146.2	109.8	76.2	89.6	67.4	60.5
bootstrap	105.8	77.9	56.0	68.3	51.7	45.7
MM runs	112.4	85.6	72.9	70.7	59.5	59.5
MM mean	110.8	83.1	69.4	72.3	58.9	55.9
Observed richness	91	66	48	60	45	39
No. of samples	84	42	42	84	42	42
No. of adults	1853	1072	781	573	378	195
No. of adults/sample	22.1	25.5	18.6	6.8	9.0	4.6
No. of singletons	31	25	14	16	13	13
No. of doubletons	7	7	7	10	9	7
No. of uniques	34	28	18	19	15	15
No. of duplicates	12	11	7	8	7	8
Sampling intensity	20.4	16.2	16.3	9.6	8.4	5.0
Inventory complete- ness	66	62	71	73	71	67
Adjusted estimate range	0.59	0.50	0.42	0.37	0.33	0.38

the curves of the latter estimator are presented here. Chao 1, Chao 2, and ICE estimator curves were also especially erratic, even at high sample numbers. Because the two Chao and Lee estimators gave unrealistically high estimates (Table 2), their curves are not presented in Figs. 1–6. Plots of singletons and uniques rise quickly, level off, and do not decline. There are always more uniques than singletons. Plots of doubletons and duplicates rise more slowly, level off, and, in some data sets (grass total and grass fall), begin to fall.

The richness estimates generated by the 11 estimators varied widely (Table 2). The two Chao & Lee estimates were always distinctively high (especially for the grass bald). The bootstrap estimates were consistently the lowest of the remaining nine estimators, and the second-order jackknife and, occasionally, Chao 1 produced the highest estimates. The estimates of the other six estimators tended to cluster more tightly and varied in rank depending on community and season. The ranges spanned by these six estimates (ACE, ICE, Chao 2, first-order jackknife, and Michaelis-Menten runs and means) are smaller for the heath bald data sets than for the corresponding grass bald sets.

These six richness estimates (106–160 for the grass bald and 68–90 for the heath) and the observed richness (91 and 60) indicate that more spider species live in the grass bald community than in the heath bald community. This conclusion is also supported by the observation that the heath bald data set produced a smaller adjusted estimate range (the ratio of the range of all but the two Chao & Lee estimators divided by the observed richness; Table 2), which suggests that the heath bald inventory is more nearly complete than is the grass bald inventory. The conclusion is further reinforced by the observation that the observed species accumulation curves for the grass bald data sets appear to be further from reaching an asymptote than are those for the corresponding heath bald data sets (Figs. 1–6). We found this same pattern when we plotted species accumulation curves using number of specimens for the independent variable instead of number of samples; at an x-axis value of 573 specimens (the total number found in the heath bald sample set), the grass bald curve is steeper than the heath bald curve. This suggests that the observed difference in

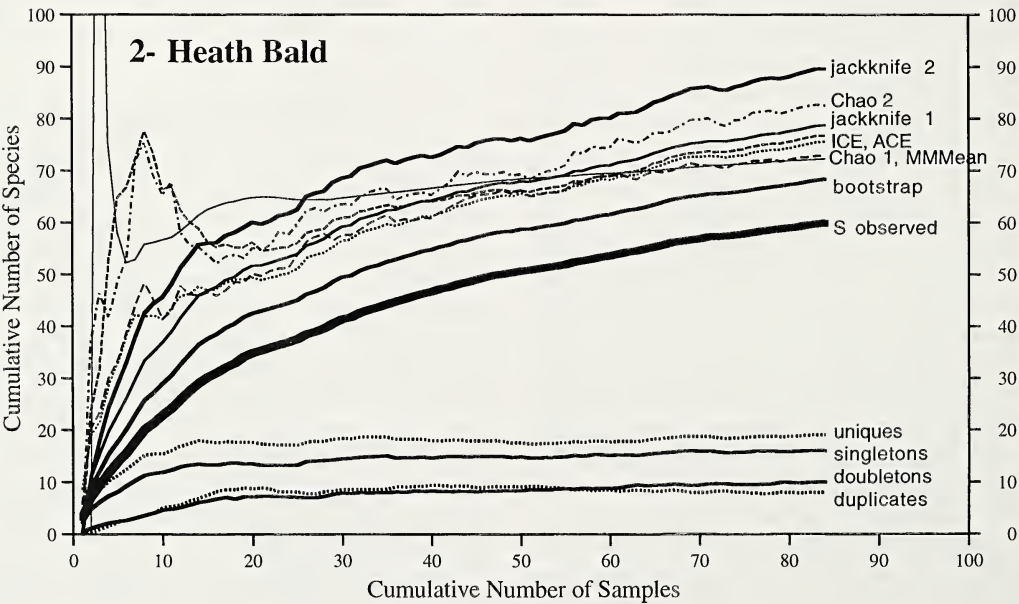
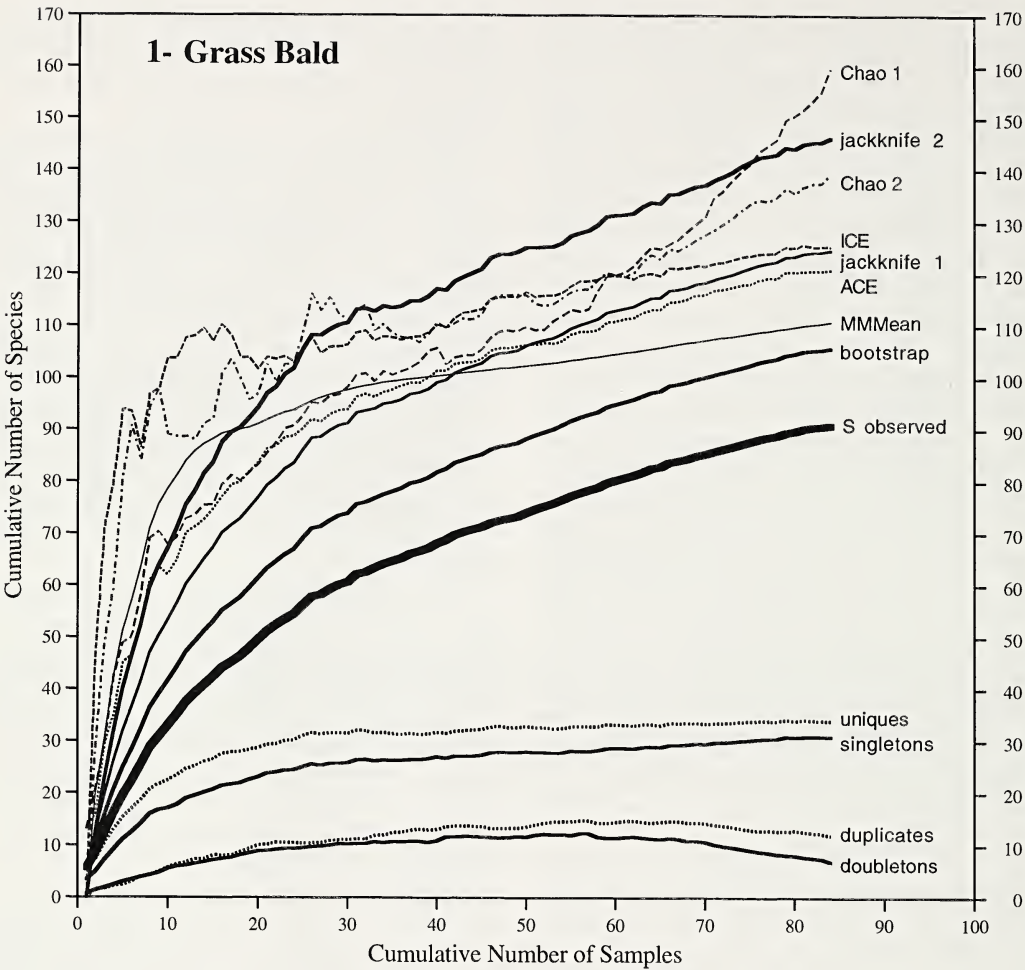
species richness between the two spider assemblages is not a result of sampling bias due to reduced sampling maneuverability in the heath bald.

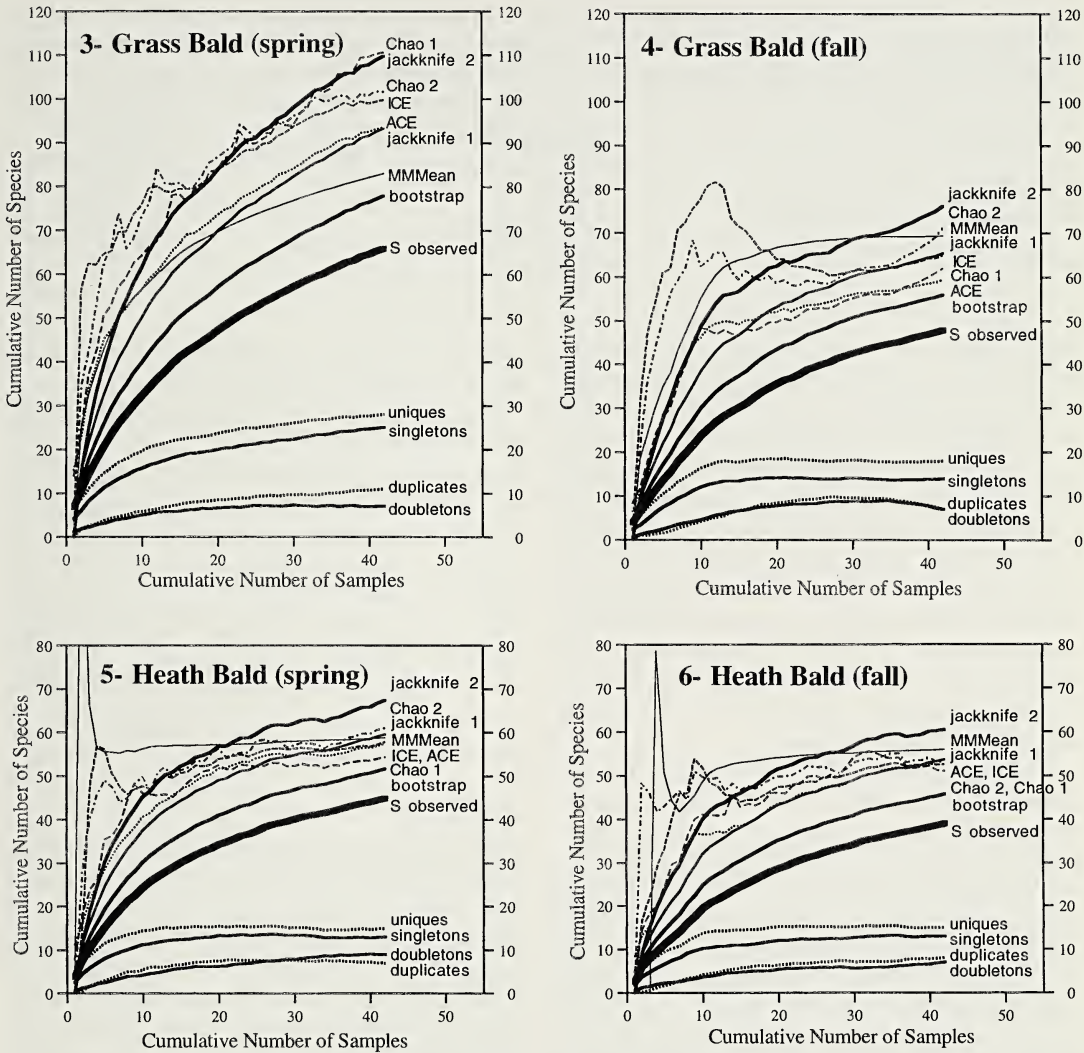
Community structure.—Values of the complementarity and similarity indices (Table 3) show that these two communities differ greatly in spider species composition; only 23 species were common to both communities. Even if the effect of “rare” species is reduced by deleting, before computing these indices, all singleton species that were found in only one community, the index values still indicate a large (although reduced) difference in species composition. In addition, there is a considerable, although smaller, difference between spring and fall samples within each community in the species present as adults (Table 3).

Both assemblages exhibit the commonly encountered skewed frequency distribution of few common species and many rare ones (Williams 1964) (Table 1). In the grass bald only 7 of the 91 observed species each comprise 2% or more of the adults collected. Of these 7 “dominant” species, one (*Ceraticelus alticeps*, an erigonine linyphiid) is superabundant, comprising 54% of all adults collected at the site. In the heath bald 19 of the 60 observed species each comprise 2% or more of the adults collected. The two most abundant of these “dominants”, *Collinsia oxypaederotipus* (an erigonine linyphiid) and *Lepthyphantes zebra* (a linyphiine linyphiid), make up 15% and 14% respectively of all adults collected.

In both communities, linyphiids were far more common than any other family in terms of numbers of species and adults (Table 4). The next three most species-rich families in the grass bald (Salticidae, Lycosidae, and Araneidae) were much less well represented in the heath bald; the absence of lycosids and the presence of only one araneid species in the heath samples are particularly noteworthy. Very small juveniles of *Araneus* orbweavers (probably *A. nordmanni*) were common in the heath; we saw only two or three large orb webs, but did not find their owners. Two families were notably more species-rich in the heath samples than in the grass bald: Dictynidae and Leptonetidae.

In the grass bald, the percentages of aerial (47) and ground-dwelling (53) species are





Figures 3–6.—Plots comparing the performance of eight estimators of species richness with the observed species accumulation curve, using data from the four sets of spider samples. 3. Spring samples from the grass bald; 4. Fall samples from the grass bald; 5. Spring samples from the heath bald; 6. Fall samples from the heath bald. Scales, line symbols, variables, and computation protocols are the same as for Figure 1.

Figures 1, 2.—Plots comparing the performance of eight estimators of species richness with the observed species accumulation curve, using data from all 84 samples (spring and fall) of spiders from the grass bald (Figure 1) and the heath bald (Figure 2). The species accumulation curve (S observed) plots the observed number of species as a function of the number of pooled samples. The eight curves above the species accumulation curve show the estimated species richness based on successively larger numbers of samples. The estimators used are ACE, ICE, Chao 1, Chao 2, first-order jackknife (jackknife 1), second-order jackknife (jackknife 2), bootstrap, and Michaelis-Menten means (MMEans). All values were generated by EstimateS, version 5.0.1 (Colwell 1997). The four curves at the bottom of the graph plot mean numbers of singletons, doubletons, uniques, and duplicates as a function of cumulative number of samples. For all 13 curves, each point is the mean of 100 values based on 100 randomizations of sample accumulation order.

Table 3.—Values of complementarity and similarity indices for the two communities and for the spring and fall data sets of each community. See text for definitions of the indices. Index values in parentheses were generated after deleting all singletons found in only one community.

	Grass bald to heath bald	Grass bald spring to fall	Heath bald spring to fall
% Complementarity	82 (73)	75	60
Kulczynski's index of similarity	0.196 (0.229)	0.584	0.363
Sorensen's index of similarity	0.305 (0.422)	0.397	0.571

about equal, and the ground web-building guild is the most species-rich (35% of all species present) (Table 5). In the heath bald, 67% of the species are ground-dwellers, with the great majority of these (58.3% of all species present) probably being ground web-builders. Pronounced seasonal changes occurred in the (adult) guild composition of the grass bald community but not in the heath community (Table 5). The number of aerial web-builder species present as adults increased and the number of aerial and ground hunter species present as adults decreased between spring and fall in the grass bald.

Collecting methods: taxonomic characterization of yields.—The complementarity matrices reveal—for both communities—generally large differences among the methods in the taxonomic composition of the spider samples these methods yield (Table 6). The smallest differences are those between ground and litter samples, beating and sweeping samples, and beating and aerial samples. In terms of number of species per sample, it appears that aerial and beating methods are the least productive (Table 7). Each method yielded some unique species not collected by any other method; aerial hand collecting in the heath yielded the smallest number of unique species (Table 7). From 33–60% of these unique-to-method species were singletons.

DISCUSSION

Species richness estimates.—The best way to test the performance of species richness estimators is to use data sets from a site where the actual species richness is known; the germinating seed bank data set used by Colwell & Coddington (1994) and Butler & Chazdon (1998) essentially meets this requirement. Unfortunately, we cannot use this direct approach to evaluate estimator performance because none of our observed species accumulation

curves reached an asymptote; evidently we have not collected all the species present as adults at either site during the seasons when we sampled. However, we can employ other less rigorous (indirect) ways to assess estimator usefulness—observing how rapidly estimation curves approach an asymptote as sample number increases (Colwell & Coddington 1994; Coddington et al. 1996; Chazdon et al. 1998), looking for a consensus among a majority of estimators (Coddington et al. 1996), and comparing the estimator curves to subjective visual extrapolations of the possible asymptotes of an observed species accumulation curve. A good estimator 1) should reach (or at least closely approach) a stable asymptote with fewer samples than are required for the observed species accumulation curve to reach an asymptote, 2) is unlikely to yield estimates that differ widely from those of all other estimators, and 3) should give estimates that are close to reasonable visual extrapolations of the asymptote of the observed species accumulation curve.

The two Chao & Lee estimators generated unrealistically large estimates, especially so with the grass bald data sets. Colwell & Coddington (1994) observed the same tendency of these two estimators to overestimate species richness with a seed bank data set. The newer, modified coverage-based estimators, ACE and ICE, the latter of which performed especially well in a recent study by Chazdon et al. (1998), generate much more realistic richness estimates for our sample sets than do the Chao & Lee estimators. Although the rankings of richness values generated by all 11 estimators vary somewhat among our data sets and from study to study (Coddington et al 1996; Silva & Coddington 1996; Dobyns 1997; Chazdon et al. 1998), the relatively tight clustering of the ACE, ICE, Chao 2, first-order jackknife,

Table 4.—Percent (of community total) of species and adults collected in each family. Number of species is in parentheses.

	Grass bald		Heath bald	
	% of species	% of adults	% of species	% of adults
Agelenidae	1.1 (1)	0.2	1.7 (1)	0.7
Amaurobiidae	3.3 (3)	0.4	6.7 (4)	4.7
Antrodiaetidae	1.1 (1)	0.4	1.7 (1)	3.7
Anyphaenidae	1.1 (1)	0.1		
Araneidae	8.8 (8)	2.1	1.7 (1)	0.2
Clubionidae	4.4 (4)	5.7	5.0 (3)	4.4
Cybaeidae			1.7 (1)	0.7
Dictynidae	2.2 (2)	0.2	8.3 (5)	5.9
Gnaphosidae	1.1 (1)	0.2		
Hahnidae	2.2 (2)	1.1	5.0 (3)	6.1
Leptonetidae			3.3 (2)	0.5
Linyphiidae	30.8 (28)	80.6	36.7 (22)	51.7
Liocranidae	1.1 (1)	0.2	3.3 (2)	3.5
Lycosidae	9.9 (9)	1.0		
Nesticidae			1.7 (1)	0.7
Oxyopidae	1.1 (1)	0.3		
Philodromidae	1.1 (1)	0.1		
Salticidae	18.7 (17)	5.0	8.3 (5)	7.3
Tetragnathidae	1.1 (1)	0.3	1.7 (1)	1.2
Theridiidae	6.6 (6)	1.6	8.3 (5)	7.3
Theridiosomatidae			1.7 (1)	1.2
Thomisidae	4.4 (4)	0.5	3.3 (2)	0.7

and Michaelis-Menten estimator values suggests that they are either estimating the same real value or are being biased in the same manner. When we apply the above-mentioned three criteria of a potentially good estimator to the performance of the estimators with all six of our data sets, the Michaelis-Menten estimator appears to perform best. ICE and ACE also perform rather well but do not approach an asymptote as quickly as the Michaelis-Menten estimator. Chao 2 and the first-order jackknife show some promise, but the former is sometimes quite unstable and neither closely approach an asymptote. The poor performance of the bootstrap estimator on our data

sets echoes the findings of others (Colwell & Coddington 1994; Chazdon et al. 1998). Although they used tropical forest seed, seedling, and sapling data sets that differed greatly from ours, Colwell & Coddington (1994), Butler & Chazdon (1998), and Chazdon et al. (1998) did not come to conclusions that were radically different from ours about the performance of these richness estimators. However, they did give ICE (Chazdon et al. 1998) and Chao 2 (Colwell & Coddington 1994; Chazdon et al. 1998) the highest overall ratings.

The failure of the observed species accumulation curve and most of the estimator curves to reach an asymptote with our data

Table 5.—Percentage of species in each guild for each community and for spring and fall samples from each community. Any species in two guilds (see Table 1) was assigned to its primary guild.

			Grass		Heath	
	Grass	Heath	Spring	Fall	Spring	Fall
Aerial web builders	22.0	21.7	12.1	31.3	17.8	15.4
Ground web builders	35.2	58.3	37.9	41.7	62.2	69.2
Aerial hunters	25.3	11.7	28.8	16.7	11.1	10.3
Ground hunters	17.6	8.3	21.2	10.4	8.9	5.1

Table 6.—Percent complementarity of the samples collected by different methods. See text for definition of percent complementarity. Number of sample units in parentheses.

Grass bald				
	Beating (24)	Sweeping (24)	Ground (24)	Litter (12)
Beating	—	70	80	87
Sweeping	—	—	80	87
Ground	—	—	—	67
Heath bald				
	Beating (24)	Aerial (24)	Ground (24)	Litter (12)
Beating	—	72	78	87
Aerial	—	—	84	90
Ground	—	—	—	57

sets is directly related to the fact that the numbers of singleton and unique species failed to decline as sample size increased (Figs. 1–6). Indeed, the relatively steep “final” slopes of the Chao 1, Chao 2, and first- and second-order jackknife curves for the grass bald data sets (Figs. 1, 3, 4) were caused by this failure of singletons and uniques to decrease with increased collecting effort while doubletons and, to a lesser degree, duplicates decreased.

Since rare species (especially singletons and uniques) play such an important role in generating most of these estimates, it may be instructive to examine the ecological and taxonomic status of singletons in our data sets. Most of the singletons in each community (55% of bald and 63% of heath singletons) are common in other habitats in the GSMNP, and most of the rest appear to be common only in regions beyond the GSMNP boundary (Table 1). Consequently, many of these species may not be permanent (breeding year after year)

members of these bald communities. However, it is also possible that some or many of these singletons may be temporal singletons, artifacts of temporally patchy sampling; we will not know without collecting early spring, summer, and late fall samples of adults from these balds. For those families represented by five or more species in either or both bald communities, the percentage of that family’s species that are singletons ranges from 22–67%: Araneidae (22%), Linyphiidae (28%), Amaurobiidae (29%), Clubionidae (40%), Salticidae (50%), Thomisidae (50%), Theridiidae (55%), Dictynidae (60%), Lycosidae (67%). Why lycosid species should more often be rarer than araneid or linyphiid species in these habitats, especially in the meadow-like grass bald, is not obvious. Sampling bias is not a likely explanation, because our ground and litter sampling methods collect large numbers of lycosid individuals and/or species in some other non-forest and forest communities in the GSMNP.

Table 7.—Comparison of total number of species and number of unique species (here defined as species collected by only one method) sampled by each method in each community. Number of samples in parentheses after each method heading. The number of unique species which are singletons is given in parentheses after the number of unique species.

Grass bald				
	Beating (24)	Sweeping (24)	Ground (24)	Litter (12)
No. of species	27	44	45	32
No. of species per sample	1.1	1.8	1.9	2.7
No. of unique species	7 (4)	20 (11)	15 (9)	11 (5)
Heath bald				
	Beating (24)	Aerial (24)	Ground (24)	Litter (12)
No. of species	23	14	38	27
No. of species per sample	1.0	0.6	1.6	2.3
No. of unique species	9 (4)	4 (2)	18 (6)	7 (3)

As in similar inventories of spider assemblages (Coddington et al. 1996; Dobyns 1997), it is difficult to judge from these data sets and estimates the true species richness at either study site, primarily because we identified and counted only adults and therefore do not know how many resident species populations consisted only of juveniles during the two brief sampling periods at each site. The diversity of phenologies in a typical spider community is so great (Toft 1976) that it may be difficult or impossible to estimate true richness until sampling bouts for adults are distributed more evenly throughout the annual cycle of seasons or juveniles are identified to species. This is demonstrated by the differences in species richness (observed and estimated) and species composition between spring and fall samples at each of our bald sites. Accurate estimation of true richness from snapshot sampling may only be feasible where spider faunas are extremely well known, because it will require either accurate sampling and identification of all age classes or the use of estimator formulas derived in part from extensive knowledge of the life cycle patterns of relevant spider assemblages. It is possible that late spring and early fall are the two best times to inventory spiders in temperate communities, and that two such samples will prove adequate for estimating species richness, but these possibilities need to be tested by year-round sampling.

One goal of species richness inventories should be to help predict how many samples are required for a complete (observed species accumulation curve reaches asymptote) or adequate (accurate estimate of true richness) survey. Indices like sampling intensity or inventory completeness may be useful. Our results indicate that one drawback of the sampling intensity index is that a superabundant species (like *Ceraticelus alticeps* in the grass bald) can inflate the index; even though our sampling intensity at the grass bald was 20.4, the species accumulation curve generated for that site was not as close to its asymptote as was the curve for the heath bald, which had a much lower sampling intensity (9.6). Excluding species with abundances of more than 100 or 200 would be a way to avoid such inflated sampling intensity values. As noted by Coddington et al. (1996), the rough estimate by Coddington et al. (1991) that a sampling in-

tensity of 10 should be adequate for an accurate survey is low, at least for some spider assemblages. The inventory completeness indices for our two fall data sets (71, 67) are comparable to that for the Ellicott Rock forest fall data set (71) (Coddington et al. 1996). While the latter data set consisted of three times as many samples as either of our fall data sets, it also contained over twice as many species. The similar slopes of the observed species accumulation curves for the forest and both fall bald data sets suggest that all three inventories may have reached roughly the same degree of completeness.

It is clear that more sampling is needed at both bald sites to determine whether any of these estimators can provide meaningful estimates of the species richness of these spider assemblages. However, a few results suggest that our heath bald inventory is more nearly complete than the grass bald inventory, in spite of roughly equal sampling effort; the heath data set yields 1) observed and estimated richness curves that are more closely approaching an asymptote, 2) smaller gaps between observed and estimated richness curves, and 3) a smaller interval between the lowest and highest richness estimates. This last result is expressed by the adjusted estimate range (Table 2), which may be a useful indicator of inventory completeness. The intensity and seasonal frequency of sampling needed to generate samples of adult spiders that may yield useful estimates of species richness will only be determined by analysis of data from concerted year-round sampling effort at a particular site and will certainly differ from region to region and habitat to habitat.

Community structure.—The large differences between these two bald spider assemblages in both taxon and guild composition are not surprising considering the big differences in community physiognomy and plant species composition. The grass bald contains large patches of low grass and herb-dominated meadow habitat not found in the heath bald; the impact of this difference in the plant component of the communities on the spider component is demonstrated by the observation that 19 (26%) of the 76 grass bald spider species found elsewhere in the GSMNP are found only in non-forested meadow habitats whereas in the heath bald this is true for only one (2%) of 54 species. The fact that many of these

meadow species are salticids, lycosids, and araneids helps explain the much better representation of these three families in the grass bald. We suggest that the very low richness and abundance of adult orb weavers in the heath bald, in spite of moderate numbers of very young juveniles, may be due to a paucity of flying insects, which we noticed while sampling in the heath. Perhaps juvenile orb weavers colonize the heath from adjacent habitats but find survival difficult. The striking dominance of ground-dwelling guilds, and especially the ground web-builders, in the heath bald may be due in part to a litter and humus layer that is thick and well-shaded (and therefore probably relatively stable microclimatically) and to the low diversity and abundance of herbivorous insects supported by the relatively unpalatable ericaceous foliage. Other studies demonstrate the positive correlation between litter depth, litter microclimate stability, and ground spider species richness (Uetz 1979; Coyle 1981). Furthermore, while sampling spiders, we observed a high density of detritivore arthropods in this heath litter. Perhaps the diterpene antifeedents and insecticides that make ericaceous leaves unpalatable to many herbivores (Rosenthal & Janzen 1979; Klocke et al. 1991; Harborne 1993) are leached out of the litter or reabsorbed by the plant before leaf abscission.

For the reasons given earlier in the Results section, we feel confident that the differences between the two sample sets in observed (91 vs. 60) and estimated (106–160 vs. 68–90) species richness mean that the grass bald spider assemblage is significantly richer than that of the heath bald. The much higher plant species richness and much more varied physiognomy (patches of meadow and shrubs, and scattered trees) of the grass bald, the dominance of relatively unpalatable foliage in the heath bald, and the greater diversity and abundance of herbivorous insects in the grass bald, are likely to be important (and interrelated) causes of this marked difference in spider species richness.

The apparent temporal shift in taxonomic and guild structure from spring to fall within each of these two spider assemblages is, of course, an artifact of our ignorance of juvenile spiders. The distinct differences in the life cycles and adult phenologies within an assemblage of spider species (Toft 1976) guarantees

that adult-only samples taken in one season will be different taxonomically from those taken from the same site at another season. The increase in aerial web-builders and the equally marked decrease in hunting guilds between spring and fall (adult) samples at the grass bald are consistent with the tendency of most north temperate araneids to be late summer and fall breeders and most north temperate hunting guild taxa to breed in the spring and early summer (Toft 1976; Gertsch 1979).

Collecting methods.—Longino & Colwell (1997) stressed the importance of using sampling methods that collect complementary sets of species. The large differences among our five collecting methods in the taxonomic composition of the samples these methods yielded, as well as the fact that even the least productive method (aerial hand sampling) collected four species not collected by any other method in the heath bald, justify their continued use in future sampling in these habitats. The very high productivity and distinctiveness of the sweep samples suggests that we were justified in substituting this method for aerial hand sampling in the grass bald. Such a substitution in the heath bald would not be appropriate; the physiognomy of the heath bald makes sweeping very difficult and is such that sweeping would probably sample the same taxa that beating does.

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DOES THE PRESENCE OF POTENTIAL PREY AFFECT WEB DESIGN IN *ARGIOPE KEYSERLINGI* (ARANEAE, ARANEIDAE)?

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ABSTRACT. Orb-web spiders may anticipate their future prey environment by detecting the presence of prey and adjusting their web building behavior accordingly. Here we investigate the effect of different prey sizes and density on the web size and mesh height of the orb webs constructed by *Argiope keyserlingi*. The experimental design allowed the transmission of prey vibrations but prevented any capture. We found that *A. keyserlingi* constructed webs more frequently in the presence of prey, but did not alter the web size or mesh height of their webs.

Keywords: Orb web, mesh height, foraging, behavior

Orb-web spiders (Araneae, Araneidae) employ remarkable flexibility in their foraging behavior. For example, following periods of starvation, orb-web spiders increase the size of their webs and attack prey less selectively while sated spiders reduce web size and reject less profitable prey (e.g., Sherman 1994; Herberstein et al. 1998; Herberstein et al. 2000). Web construction is energetically the most expensive component of a spider's foraging effort (Opell 1998), and webs cannot be modified following completion. Decisions made during web construction influence subsequent capture success until a new web is built. Thus, it may be advantageous to design a web in anticipation of the future prey environment, rather than simply relying on past events.

Web-building spiders may make some preemptive foraging decisions in response to the density or size of potential prey. Sandoval (1994) concluded that the orb-web spider, *Parawixia bistriata* is able to exploit swarms of unusually large termite prey. *Parawixia bistriata* typically constructed small, finely meshed webs at night that trapped tiny dipteran prey (Sandoval 1994). At the onset of the rainy season, the spiders dramatically changed their activity patterns and web design. At this time, they built additional webs during the day with increased web area and mesh height (the average distance between capture spirals). Interestingly, the spiders seemed to anticipate the timing of the swarms: they changed their web design before the ter-

mites emerged, potentially using rainfall and humidity as cues (Sandoval 1994). Experimental evidence also suggests that spiders vary mesh height due to the presence of differently sized prey (Schneider & Vollrath 1998). In a similar case, *Zygiella x-notata* (Pasquet et al. 1994) anticipated prey density before web construction. More abundant potential prey induced the construction of smaller webs earlier in the evening. Presumably, smaller webs were finished more quickly, allowing prey capture to commence earlier.

Here, we examine the effect of the size and number of potential prey on the web building behavior of *Argiope keyserlingi* Karsch 1878. We predict that larger potential prey will induce increased mesh height, and that higher prey density will decrease web area.

Experiments were conducted in March and April 1998 and January 1999, using adult *Argiope keyserlingi* collected in Sydney and Brisbane, Australia. In the laboratory, spiders were housed in upturned plastic cups (13.5 × 9 × 9 cm) where they were watered and fed blow flies (*Lucilia cuprina*, Diptera) ad libitum. The spiders were unable to construct a functional web in the upturned cups apart from a few supporting threads. Thus, prey capture did not involve a web. Instead, the spiders generally grasped the flies buzzing around in the cup.

The spiders were starved for four days prior to experimentation. This ensured that the spiders' energetic status was uniform. Addition-

ally, by depriving spiders of web-building space we minimized the influence of previously built webs on the foraging decisions made during experimentation (see Herberstein et al. 2000). The spiders were weighed and transferred to three-dimensional frames ($40 \times 50 \times 8.5$ cm) and allowed to construct complete webs in the presence of different sizes and densities of potential prey. Frames either contained 30 *Drosophila* (Diptera), one blow fly, or 30 blow flies. Prey were held in identical plastic jars (diameter: 4.7 cm, height: 6.8 cm), covered by fine mesh. This setup allowed prey movement and the transmission of airborne vibrations created by the buzzing of the flies, but prevented capture.

We selected the two prey types because they differ in body length (blow flies: 7.8 ± 0.12 mm, $n = 20$; *Drosophila*: 2.5 ± 0.06 mm, $n = 20$). To control for differences in weight and therefore energy return, treatment one consisted of 30 *Drosophila* per jar. This approximated the weight of one blow fly per jar as used in treatment two (one blow fly: 0.022 ± 0.0006 g, $n = 39$; 30 *Drosophila*: 0.021 ± 0.0004 g, $n = 21$). The third treatment, 30 blow flies, allowed comparison of the webs built for different prey densities, and for different prey types. Only the first web spun by each individual was measured and used to evaluate the effects of the prey treatments. This minimized the influence of previous foraging history on web design. We estimated the web area and the mesh height using various formulae that only require a few measurements (Herberstein & Tso 2000).

Statistical analyses were conducted using Systat 5.2 (Wilkinson 1992) and G•Power (Buchner et al. 1997). Data were log transformed if they were not normally distributed (Kolmogorov-Smirnov). Web area, mesh and spider weight were compared using ANOVA with treatment and year as factors. All values are mean \pm SE unless stated otherwise.

Data from 49 spiders were included in the analyses. There was no significant difference in body weight between the spiders used in 1998 and 1999 (for 1998/1999: 30 blow flies 0.255 ± 0.028 g / 0.266 ± 0.023 g, one blow fly 0.269 ± 0.020 g / 0.293 ± 0.029 g, 30 *Drosophila* 0.253 ± 0.019 g / 0.219 ± 0.038 g; $F_{1,43} = 0.00001$, $P > 0.05$). The weight of spiders allocated to the three treatments was similar ($F_{2,43} = 1.37$, $P > 0.05$), and there

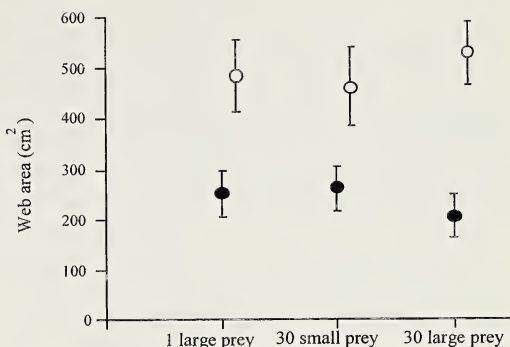


Figure 1.—The mean (\pm SE) area of webs constructed in the presence of one large prey, 30 small prey and 30 large prey in 1998 (●) and 1999 (○).

was no interaction effect of year and treatment ($F_{2,43} = 0.61$, $P > 0.05$). Web area (Fig. 1) did differ between the two years ($F_{1,43} = 30.79$, $P < 0.01$): in 1999 spiders constructed larger webs compared to the previous year. This is probably because spiders were maintained in the laboratory for approximately two months before use in 1998, whereas the experiment was commenced within two weeks of collection in 1999. Varying the size and density of potential prey did not affect web size ($F_{2,43} = 0.007$, $P > 0.05$), nor was there an interaction effect between year and treatment ($F_{2,43} = 0.79$, $P > 0.05$). The size of the frame, and thus the available web building space may have limited the foraging decision of the spiders. However, the maximum web size observed (approx. 850 cm^2) was less than half of that available (2000 cm^2).

Mesh height (Fig. 2) was similar in both years ($F_{1,43} = 1.40$, $P > 0.05$) and was unaffected by prey treatment ($F_{2,43} = 0.34$, $P > 0.05$). Contrary to prediction, the presence of large prey did not result in larger mesh height compared to small prey. Power analysis revealed that our sample size was sufficient to detect a treatment effect ($1 - \beta = 0.68$). Again, the interaction between year and treatment was not significant ($F_{2,43} = 1.63$, $P > 0.05$).

These results are contrary to both of our predictions, and the results of previous studies (Schneider & Vollrath 1998; Pasquet et al. 1994) that found a relationship between the size and density of prey and web design. However, these previous experiments released prey into the web-building frames with the spiders. In the laboratory, we frequently ob-

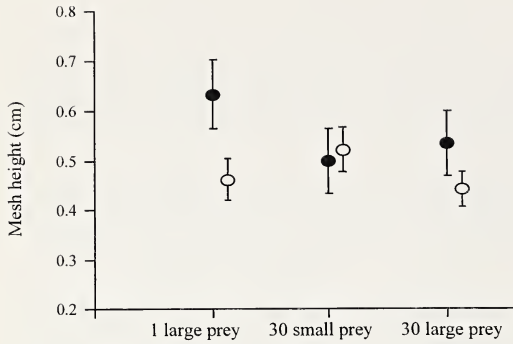


Figure 2.—The mean (\pm SE) mesh height for webs constructed in the presence of one large prey, 30 small prey and 30 large prey in 1998 (●) and 1999 (○).

serve orb-web spiders housed in both frames and cups grasping and consuming prey without webs. As the spiders in these previous experiments (e.g., Schneider & Vollrath 1998) had the opportunity to capture prey during web building, it is unclear whether their webs represented an anticipatory prey assessment, or past experience. In the present study, enclosing the prey in mesh-covered jars prevented such confounding effects. However, the absence of any significant difference in web design between the prey treatments suggests two explanations; either our experimental design did not allow the spiders to detect the prey, or *A. keyserlingi* does not make preemptive adjustments to web mesh size and area to suit varying sizes and numbers of potential prey.

To distinguish between these two explanations, we repeated the experiments in January and May 2000 using identical methods but including a control treatment (no flies), where we measured web area and mesh height in a sub-sample and the frequency of web construction in a larger sample of individuals. We predicted that, if these spiders can detect airborne vibrations created by the enclosed flies, we should find differences between treatments that included no blow flies (empty container), one blow fly and 30 blow flies. Any difference in the web-building behavior between the no-fly treatment *versus* the fly treatments would indicate that the spiders were able to detect the presence or absence of prey in the containers.

We found no significant differences in mesh size ($F_{2, 34} = 1.28, P > 0.05$) or web

Table 1.—The mean (\pm SE) for the web area and mesh height of spiders constructing webs when there are no flies, one fly or 30 flies enclosed with the spider.

Treat- ment	Sam- ple size	Web area (cm ²)	Mesh height (cm)
No flies	11	1053.0 \pm 112.6	0.517 \pm 0.02
1 fly	12	1015.3 \pm 108.4	0.503 \pm 0.04
30 flies	14	1086.8 \pm 100.3	0.517 \pm 0.02

area ($F_{2, 34} = 0.29, P > 0.05$; Table 1) between the treatments. However, fewer spiders constructed a web when no flies were present (16 out of 24 spiders). In contrast, almost all spiders (21 out of 22) presented with a jar of 30 blow flies, and 19 of 26 spiders presented with only one blow fly, built a web. We compared these frequencies using a contingency table, which revealed that the likelihood to build a web was significantly different between the three treatments ($\chi^2 = 6.3, P = 0.044$). These results indicate that our experimental design allowed the spiders to detect the presence of potential prey, and they adjusted the frequency of web construction accordingly (see also Pasquet et al. 1994), but not web size or design. It may be that spiders are unable to detect differences between the airborne vibrations created by different sizes and densities of prey. Alternatively, spiders may be able distinguish between prey densities and sizes, but do not alter the web design in response. Behavioral tests, such as those presented here, cannot distinguish between these two alternatives.

Adjusting web building frequency in response to the presence of prey may reflect risk sensitivity, where foragers react to variation in prey encounter rates by changing web sites or web size (e.g., Herberstein et al. 2000; Gillespie & Caraco 1987). Web building spiders invest a substantial amount of energy into silk production and web construction (e.g., Peakal & Witt 1976; Higgins & Buskirk 1992), and rely on prey coming into contact with the web. As such, prey encounter can be highly unpredictable and spiders may conserve energy by not building a web when there is little indication of abundant prey. In contrast, when prey is in close proximity and in high density,

increased web building activity may allow these spiders to exploit abundant prey.

Numerous field studies have also failed to find a consistent relationship between mesh height and prey size (McReynolds & Polis 1987; Herberstein & Elgar 1994; Herberstein & Heiling 1998). Simulations (Eberhard 1986) and laboratory manipulations (Nentwig 1983) further confirm that orb-webs do not function as "sieves." Mesh height may fulfill alternative functions. A narrow mesh may facilitate the retention of larger prey, as more threads are in contact with the item (Eberhard 1990). However, more spiral turns also reflect more light thus increasing the visibility of the web to prey (Craig 1986; Craig & Freeman 1991). Mesh height may therefore indicate a compromise between prey retention and web visibility. A larger capture area results in a higher prey interception rate (Chacón & Eberhard 1980) and by increasing the distance between sticky spirals spiders may enlarge overall capture area without greater energy expenditure. Accordingly, food deprived spiders commonly increase web area to enhance prey encounter (Sherman 1994; Herberstein et al. 2000). Finally, it seems unlikely that spiders would tailor their webs for small and possibly unprofitable prey. Spiders often ignore small prey entangled in the web (Uetz & Hartsock 1986; Herberstein et al. 1998) which may subsequently escape. Logically, any web should target profitable prey items worthy of attack and more permanent retention through silk wrapping.

Web design reflects several trade-offs between the different functions of various web elements and is influenced by internal physiological states and previous experience. Interpreting orb-webs as size filters is likely to oversimplify this complex foraging investment.

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SHORT COMMUNICATION

ADANSONIA IS A BAOBAB TREE, NOT A THERIDIID SPIDER

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ABSTRACT. The name *Adansonia* Saville-Kent was erroneously introduced into spider taxonomy by Bonnet in 1939 and still appears in the literature. Saville-Kent was referring to a tree, not describing a spider.

Keywords: Theridiidae, Araneae, *Adansonia*, nomenclature, systematics

Most biologists are familiar with the genus *Adansonia* Linnaeus 1753, which contains the magnificent Baobab trees. The Baobabs are particularly prolific in Madagascar but also widely distributed in continental Africa, and one species is native to northwestern Australia. These trees are also popular in botanical gardens and parks in other parts of the world. Less well known is the mollusk *Adansonia* Pallary 1902. Pallary validly proposed this name as a subgenus of *Donovania* Bucquoy Dautzenberg & Dollfus, which in turn is now considered a junior synonym of the buccinid snail *Chauvetia* Monterosato. Very few are aware of yet another use of the name *Adansonia*, but *Adansonia* Saville-Kent 1897 is currently listed as a generic name of the spider family Theridiidae (Platnick 1997). The latest use of the name is an error that can be traced back to a cataloging mistake by Bonnet (1939). This note is written to clarify the situation and prevent further inclusion of the name *Adansonia* Saville-Kent in spider taxonomy.

The acclaimed author of the name is William Saville-Kent (1845–1908), whose works include “The Great Barrier Reef of Australia” (Saville-Kent 1893) and “The Naturalist in Australia” (Saville-Kent 1897). In the latter he was discussing a theridiid spider:

“A remaining spider form included in Chromo-Plate IX. invites brief notice. It is represented by Figs. 12 to 15 [these show the details of the egg cocoon and the general habitus of the spider]. This type is apparently referable to the genus *Theridium*, and is remarkable more especially with relation to its habits and the singular environments of its egg cocoon. It

was observed by the writer in the neighbourhood of Derby, at the head of King’s Sound, Western Australia, taking up its abode in the fissures of the gnarled trunks of the older Baobab or Bottle-trees, *Adansonia rupestris*. The spider, a small brown one, presents no special features of interest, and neither does the web, which is of the irregularly meshed order. Suspended in the snare, however, there is generally present a little cupola-shaped mass, which, on near examination, is found to be composed superficially of the emptied skins and disjointed limbs of a small species of black ant upon which this spider habitually feeds. The interior of this ant aggregation is hollow, and is found to contain in its upper confines the spherical silken egg cocoon of its fabricator, which it has most effectively and ingeniously concealed from view” (Saville-Kent 1897:261).

It is clear from Saville-Kent’s text that he did not intend to describe a new species, and thus gives the spider no name, he is simply sharing some interesting observations with the reader. Bonnet (1939), however, mistakenly connected Saville-Kent’s description of the spider to the Latin name of the Baobab and listed *Adansonia* Saville-Kent, as a new genus and *Adansonia rupestris* Saville-Kent as a new species (which he designated as the type species, by monotypy), in the family Theridiidae (Bonnet 1939:158)! Bonnet’s error does not appear in Levi & Levi’s (1962) exhaustive work on theridiid genera, nor in the catalogs of Roewer (1942), Brignoli (1983) or Platnick (1988), but *Adansonia* is listed as a theridiid genus in the two most recent spider taxonomy catalogs under the heading of “No

Entries" (Platnick 1993:180; 1997:248). Thus no one has used this name since Bonnet's error.

The argument might be made that Bonnet's error can be considered as providing availability to *Adansonion rupestris* Saville-Kent. To be available, every new name published after 1930 must be accompanied by a bibliographic reference to a description that states in words, characters that are purported to differentiate the taxon (International Commission of Zoological Nomenclature, 1999: Art. 13.1.1 & 13.1.2). Thus Bonnet would make *Adansonion rupestris* available because he provides a reference to a description. However, Saville-Kent does not provide a description of the spider, "The spider . . . presents no special features of interest and neither does the web . . ." (Saville-Kent 1897:261) but rather of the egg cocoon. The egg cocoon is the work of an animal and is clearly excluded from zoological nomenclature (International Commission of Zoological Nomenclature, Art. 13.6.2). Therefore, it is clear that by the publication of *Adansonion* in Bonnet's (1939) catalog Bonnet was not making a new name available; he was merely cataloging what he thought was Saville-Kent's new name (*Adansonion rupestris*). But as there is no new Saville-Kent name, Bonnet does not accidentally validate a name. It is furthermore clear that *Adansonion* was in use for a mollusk genus (Pallary 1902) at the time of Bonnet's publication and is therefore unavailable regardless of other things due to the principle of homonymy (International Commission of Zoological Nomenclature, 1999: Art. 52.1, 52.2 & 52.3). *Adansonion* Saville-Kent is thus a *nomen nudum* and *Adansonion rupestris* is a tree.

After the removal of *Adansonion* there are currently 73 valid genera in the family Theridiidae (Platnick 1997; Tanikawa 1998).

I would like to thank Mark Harvey for making a copy of Saville-Kent's paper available to me and with his help in locating Bonnet's error. Chris Thompson provided valuable help on nomenclatural issues. Gustavo Hormiga, Mark Harvey, Chris Thompson, Jonathan A. Coddington, Petra Sierwald, Matjaz Kuntner and Jeremy Miller provided comments on the manuscript. Support for this research was provided by a National Science Foun-

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SHORT COMMUNICATION

***METOPIA SINENSIS* (DIPTERA, SARCOPHAGIDAE), AN UNUSUAL PREDATOR OF *LIPHISTIUS* (ARANEAE, MESOTHELAЕ) IN NORTHERN THAILAND**

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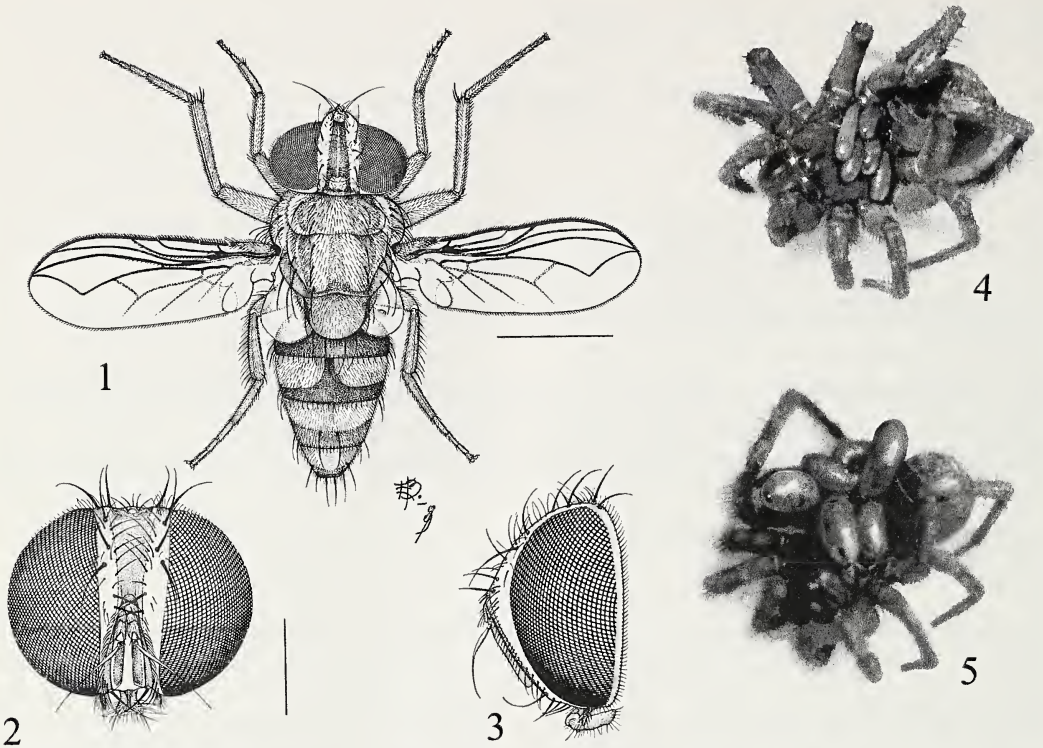
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Keywords: *Liphistius*, *Metopia*, predator, Thailand

Knowledge on predators, parasites and parasitoids of the Mesothelae is sparse and fragmentary. Various authors reported on gamasid and erythraeid mites, mermithid nematodes and *Rickettsia* infesting either adult mesothelid spiders or their egg cases (Bristowe 1933; Yoshikura 1954; Platnick & Sedgwick 1984; Haupt 1979 & pers. comm.). Sedgwick & Platnick (1987) found a wasp pupa in an abandoned burrow of *L. endau* Sedgwick & Platnick 1987 in Malaysia, and Bristowe (1976) reported the observation of an unidentified pompilid wasp larva attached to the abdomen of a paralysed *L. desultor* Schiödt 1849 found inside its burrow on Penang Island, Malaysia. The latter author further mentioned empty pupal cases of a fly among the old fragments of *L. bristowei* Platnick & Sedgwick 1984 (misidentified as *L. birmanicus* Thorell 1897) in Thailand, probably on Doi Suthep (Mount Suthep), Chiang Mai, northern Thailand (cf. Bristowe 1975). Recently one of us (PJS) found puparia and imagines of *Milichia* sp. (Diptera, Milichiidae, det. by J. Chainey, The Natural History Museum, London) among partly devoured eggs of *L. yamasakii* Ono 1988 in northern Thailand. Also puparia of another cyclorrhaphan fly were collected from several empty burrows of *L. bristowei* on Doi Suthep and nearby Doi Inthanon, but no imagines could be obtained for a proper identification (Schwendinger 1990). Later Schwendinger (1998) reported a second, more

fortunate find. Imagines of *Metopia sinensis* Pape 1986 (Figs. 1–3; specimens deposited at the Swedish Museum of Natural History, Stockholm), a miltogrammine flesh fly, were raised from larvae infesting three or four carcasses of *L. lahu* Schwendinger 1998 inside the spider burrows at Doi Angkhang, about 150 km north of Doi Suthep. The fly species was at that time known only from a single specimen from southern China (Pape 1986a, 1996). The observation was cautiously interpreted as a case of carrion feeding rather than predation or parasitism (Schwendinger 1998) because species of *Metopia* Meigen 1803 are known to be kleptoparasites in nests of solitary aculeate Hymenoptera (Pape 1986b, 1987; Spofford et al. 1989). The fly larvae feed on prey stored for the host progeny. New observations reported and discussed in the following, however, indicate that *M. sinensis* very likely is a primary predator.

In December 1997 PJS again found fly puparia of *M. sinensis* in two empty *Liphistius* burrows (near the Thai-Myanmar border in Mae Hong Son Province, northern Thailand) in a colony of an undescribed species closely related to *L. lahu*. All puparia had already hatched; but one of the spiders collected, a lively and seemingly healthy female with a new egg case, carried six tiny fly larvae ventrally between its leg coxae. The next day (after transferring the spider to a laboratory in Chiang Mai) the spider was found motionless



Figures 1–5.—*Metopia sinensis*. 1. Male, habitus, dorsal view; 2. Male, frontal view of head; 3. Male, left lateral view of head. Note very large eyes, taking up almost entire side of head, and strongly-receding head profile with numerous facial bristles along the antenna. 4. Larvae of *Metopia sinensis* feeding on a dying *Liphistius* sp. female, second day after collecting; 5. Same, on third day after collecting. Scales: 1 = 2.0 mm; 2, 3 = 0.8 mm.

and apparently dying, and by evening the larvae had moved onto the posterior part of its carapace (Fig. 4). On the fourth day the fully grown larvae (Fig. 5) abandoned the dead spider after having devoured most of the tissues inside the prosoma and anterior opisthosoma. On the fifth day all larvae pupariated, four directly on the spider carcass, the remaining two in the container, a short distance away from the spider. Seventeen days later five imagines hatched, the sixth in the morning of the 18th day. The two male and four female flies were kept alive for two more days, during which they behaved quite atypically for sarcophagid flies: flying clumsily and unwillingly, most of the time hiding among the substrate. This may, however, be an aberrant behavior due to unnatural conditions in the laboratory. A search for *M. sinensis* at the same locality during two days in December 1998 was unsuccessful. All spiders examined were unaffected, no puparia were found and no adult flies were

attracted to three live *Liphistius* females (deposited in the Natural History Museum of Geneva) dug out of their burrows and placed as bait in uncovered containers.

Species of *Metopia* are known to be kleptoparasites in nests of various aculeate wasps and bees of the families Pompilidae, Sphecidae and Halictidae (very rarely also Vespidae), and the particular fly species seem to have a broad spectrum of hosts (Spofford et al. 1989). The flies have been classified as “hole-searchers” (e.g., Evans 1970; Spofford & Kurczewski 1990), which means that females search for host nest entrances rather than trail the wasps themselves. The female flies may larviposit into the host burrow, either standing on the rim or flying low over the hole, and the larvae then wriggle down to the stored prey of the wasp. Or, the flies may enter the burrow to larviposit near or even onto the food source. The odor of the wasp presumably triggers gravid flies to larviposit after they

have located the entrance of a host burrow (Endo 1980a,b). Being "hole-searchers," species of *Metopia* pay only little attention to prey specimens that are dragged or otherwise transported by a potential host wasp. However, individual wasps dragging prey close to the nest, and even more so those excavating burrows, may be attractive to female *Metopia*. The prey itself is not used as substrate for larviposition before it is deposited in the burrow, but female flies may occasionally larviposit directly onto the adult wasp. The latter apparently always turns out to be fatal for the fly larvae (Endo 1980a).

The present observations are considered unambiguous evidence that the association between *M. sinensis* and *Liphistius* spp. is not simple carrion-feeding. The possibility that the *Metopia* larvae were deposited on a spider left insufficiently paralyzed by a pompilid wasp is not considered very likely as the infested spider appeared in full vigor. Also, the repeated finds of flesh-fly puparia, here tentatively attributed to *M. sinensis*, in *Liphistius* burrows show that the association is persistent in time and not just a haphazard or freak larviposition. Note that the find of fly puparia by Bristowe (1976) may also refer to *Metopia sinensis*. We have decided to classify *M. sinensis* as a predator rather than a parasite (or parasitoid), following Price's (1980) definition, which states that a parasite is primarily "an organism living in or on another living organism." As the larvae of *M. sinensis* apparently kill the spider and complete most of their larval life on the carcass, they behave more like predators, even if grossly outsized by their prey.

The predator-prey association between *Metopia sinensis* and *Liphistius* most likely developed from kleptoparasitism. Sparse information from the literature and observations in Thailand by PJS indicate that pompilid wasps attack and paralyze *Liphistius* directly inside the spider burrows. In the case of *M. sinensis*, however, it appears that the wasps have completely lost their role as food providers for the fly larvae.

Predation appears to be rare or local and, at least in northern Thailand, confined to only a few *Liphistius* species. Other *Liphistius* species in the same area (i.e., *L. yamasakii* and *L. lannaianus* Schwendinger 1990) and species elsewhere in Thailand were repeatedly

observed and collected in moderate numbers by PJS during more than seven years, yet none of them was ever seen affected by *M. sinensis*. In this context, it is interesting that the infested burrows of *L. lahu* at Doi Angkhang were only about 2 km away from a thriving population of *L. lannaianus*. On Doi Inthanon, fly puparia (presumably of *M. sinensis*) were collected from scattered burrows of *L. bristowei* at 1250 m, but not found in the dense colonies of *L. yamasakii* 350–530 m higher up. From the same mountain, at 1000 m, 11 flies were also raised from the carcass of a mygalomorph spider, *Damarchus* sp. (Nemesiidae), found inside its burrow. The flies were identified as *Metopia* sp. by Nigel Wyatt (The Natural History Museum, London) and possibly also belong to *M. sinensis* (specimens unfortunately lost after identification).

While local prey specificity cannot be ruled out, a broader prey spectrum seems very likely considering the known distributional range of *M. sinensis*, which is much larger than that of its known prey. *Liphistius bristowei*, *L. lahu* and the related undescribed species are at present known only from northern Thailand; the latter two probably also occur across the border in Myanmar.

We thank Joachim Haupt (Berlin) for providing literature and for sharing his unpublished observations on pathogens and parasites of mesothelid spiders with us. Nigel P. Wyatt and John Chainey (both London) provided help with certain identifications, and Torbjörn Kronestedt (Stockholm) and Nikolaj Scharff (Copenhagen) kindly commented on the manuscript. Mrs. Elisabeth Binkiewicz skillfully produced the illustrations of *Metopia sinensis*.

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SHORT COMMUNICATION

THE USE OF FRUITS BY THE NEOTROPICAL HARVESTMAN *NEOSADOCUS VARIABILIS* (OPILIONES, LANIATORES, GONYLEPTIDAE)

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Keywords: Diet, fruits, harvestmen, *Neosadocus*

Harvestmen are solitary, nocturnal foragers that have a variety of feeding habits, ranging from scavenging to predation (see review in Gnaspini 1996). Although harvestmen seem to be generalist omnivorous arthropods, accepting both plant and animal matter, several species show a tendency to carnivory (Bristowe 1949; Capocasale & Bruno-Trezza 1964; Anuradha & Parthasarathy 1976; Gnaspini 1996; Machado et al. 2000). Reports of frugivory in harvestmen are scarce and in general are restricted to captive animals (Capocasale & Bruno-Trezza 1964; see also Gnaspini 1996). In this paper we provide the first detailed account of frugivory by a harvestman species, and investigate if fruit size and chemical content of the fleshy portion can influence fruit use by the harvestmen.

The study was conducted from October 1995 to February 1997 in the lowland forest of the Parque Estadual Intervalos (24°14'S, 48°04'W), a 490 km² reserve located in the Ribeira Valley, São Paulo state, southeast Brazil. The study site (Saibadela Research Station, elevation 70 m) receives about 4200 mm of rainfall a year, with no month receiving less than 100 mm. Rainfall, however, is less intense and less frequent between April and August, when the temperature may drop to nearly 10 °C (mean \pm SD = 20.8 °C \pm 2.5 for the study period). This period contrasts with the wetter period (September–March) when temperatures may reach 42 °C (25.7 °C \pm 2.8).

The vegetation is predominantly composed of old-growth forest (*sensu* Clark 1996) with an open understory and trees reaching up to 30 m.

The fruits of the following trees were used to investigate frugivory in harvestmen: *Virola oleifera* (Myristicaceae), *Eugenia stictosepala* (Myrtaceae), *Cabralea canjerana* (Meliaceae), *Citharexylum myrianthum* (Verbenaceae), *Alchornea glandulosa* and *Hyeronima alchorneoides* (Euphorbiaceae), throughout this paper referred to only by their generic names. Besides their availability, these fruits were selected for study because (1) they fall within three discrete size classes commonly found in tropical forests (Corlett 1996; see Table 1); (2) all of them are covered by a thin skin which allows the exploitation by harvestmen, and (3) they fit within two distinct extremes relative to the lipid content of their fleshy portions; the arils of *Virola*, *Cabralea* and *Alchornea* are lipid-rich, while the pulps of *Eugenia*, *Citharexylum* and *Hyeronima* are lipid-poor (Table 1). The fruits of *Eugenia*, *Citharexylum* and *Hyeronima* are drupes bearing one (*Eugenia* and *Hyeronima*) or two seeds (*Citharexylum*). The fruits of the remaining species are capsules that open to expose the 1–12 fruits, i.e., seeds coated by red (*Virola* and *Alchornea*) or orange (*Cabralea*) arils. These fruits are eaten by birds, monkeys and/or bats which frequently drop many fruits under the parent plants (Galetti 1996; Pizo

Table 1.—Fruit maturation period, morphology, size class (following Corlett 1996) and chemical composition of the six fruits studied. Morphological values are means \pm SD. At least 20 fruits of each species were weighed. L = lipids, P = protein, TC = total carbohydrate (i.e., soluble + structural carbohydrates). Lipids, proteins and ashes were analyzed according to the methods described in Bligh & Dyer (1959), AAC (1995, method # 46-13) and AOAC (1984, method # 22027), respectively. Total carbohydrates were obtained by difference.

Fruit	Maturation period	Morphology		Size class
		Total weight (g)	Fresh weight of pulp/aril (g)	
<i>Hyeronima</i>	Mar-Apr	0.05 \pm 0.01	0.03 \pm 0.01	small
<i>Alchornea</i>	Oct-Nov	0.09 \pm 0.01	0.03 \pm 0.01	small
<i>Citharexylum</i>	Feb-Mar	0.9 \pm 0.2	0.7 \pm 0.2	medium
<i>Cabralea</i>	Sep-Dec	0.9 \pm 0.3	0.09 \pm 0.02	medium
<i>Eugenia</i>	Apr-May	5.8 \pm 1.2	2.1 \pm 1.0	large
<i>Virola</i>	Jul-Oct	3.5 \pm 1.2	1.1 \pm 0.5	large

1997). The period of fruit maturation for the six plant species is presented in Table 1.

Voucher specimens of the harvestman were deposited in the Museu de Zoologia da Universidade de São Paulo (MZUSP), and plants at the herbarium of the Universidade Estadual Paulista at Rio Claro (HBRC).

We made diurnal and nocturnal censuses (35 days) of the harvestmen attending fresh fruits placed on the forest floor along a transect established 1–2 m off one of the trails that crossed the study site. One hundred fruits of *Virola* and 50 fruits of the other five species were set along the transect 5 m apart. Each fruit was protected from vertebrate removal by wire cages (15 \times 15 \times 10 cm, 1.5 cm mesh) closed on the top and staked to the ground. Plastic wraps placed on the top of cages protected fruits and harvestmen from being disturbed by light to moderate rains. No census was conducted under heavy rains for which the plastic shelters were useless. Fruits were set on the transect at 0800 h and checked at four-hour intervals throughout a 24 hour period. The daily light period at the study site span from 0600–1800 h, thus rendering two diurnal and two nocturnal censuses.

Only one harvestman species, *Neosadocus variabilis* (Mello-Leitão 1935), was recorded on the fruits. Individuals of *N. variabilis* were observed exploiting fruits of *Cabralea*, *Alchornea*, *Eugenia*, and *Virola* (Table 1). No harvestman was seen consuming fruits of *Citharexylum* and *Hyeronima*. Large fruits as a whole were more exploited than smaller ones ($\chi^2 = 10.94$, $df = 1$, $P < 0.001$; medium

and small fruits combined). Although there is a tendency for the harvestmen to exploit lipid-rich fruits as compared to lipid-poor ones (5.5% vs. 2.0%, respectively), the difference did not reach statistical significance ($\chi^2 = 2.73$, $df = 1$, $P = 0.09$). *Neosadocus variabilis* seems to be a strictly nocturnal forager since it was recorded only during the night censuses, i.e., from 2000–0400 h. Individuals fed on the pulp or aril of the fruit on the spot, never displacing them.

Although Walker (1928) stated that harvestman diet can consist of fruit juices and other plant-derived matter, few studies have documented fruit use by species of the order. Edgar (1971) observed the palpatorid *Leiobunum vittatum* (Say 1821) feeding on a ripe wild raspberry and, among the Laniatores, *Acanthopachylus aculeatus* (Kirby 1819) accepts papaya in the laboratory (Capocasale & Bruno-Trezza 1964), while *Neosadocus variabilis* was seen eating fallen fruits in the field (Gnaspini 1996; this study). Despite the scarcity of records, the exploitation of fallen fruits by ground-dwelling harvestmen is possibly more common than previously thought, especially for those species inhabiting tropical rainforest where a great amount of fleshy fruits is produced on a year-round basis (Jordano 1993). At our study site, for example, more than 500 kg/ha/year of fleshy fruits reach the forest floor (Pizo unpubl. data) almost continuously through the year (Morellato et al. 1999).

Results regarding the choice of fruits by *N. variabilis* based on their size and lipid content

Table 1.—Extended.

Percent of water	Chemical composition (percent of dry mass)			% of harvestmen visiting
	L	P	TC	
85.6	7.9	6.3	—	0
43.3	68.4	7.6	21.7	2
81.4	6.3	6.8	82.7	0
47.7	70.8	10.3	16.5	2
77.9	5.2	8.5	85.5	6
62.7	61.8	4.6	32.1	9

must be interpreted cautiously since small fruits are rapidly removed by ants (Pizo & Oliveira 2000), thus becoming unavailable for harvestmen. In any case, large fruits may represent more attractive food sources because they bear a great amount of fleshy material, either pulp or aril (Table 1). The use of lipid-rich fruits by harvestmen, on the other hand, deserves further investigation. In our study, *N. variabilis* exploited all the three lipid-rich fruits tested, and only the largest lipid-poor fruit. The fruits tested also differ in their carbohydrate content. This is expected since lipids and carbohydrates are highly negatively correlated in our fruit sample (Spearman rank correlation: $r_s = -0.90$, $n = 3$, $P = 0.03$), as usually occurs for fleshy fruits in general (Jordano 1993; Pizo & Oliveira 2000). There is no *a priori* reason to suspect that harvestmen would avoid carbohydrate-rich fruits. The emphasis on the role of the lipid content of the fruits in their use by harvestmen, on the contrary, is justified because it has been shown that lipid-rich fruits serve as food for carnivorous arthropods such as ponerine ants (Horvitz & Beattie 1980; Pizo & Oliveira 1998, 2000), and also attract other non-frugivorous arthropods, e.g., cockroaches and grasshoppers (Pizo unpubl. data). Carroll & Janzen (1973) hypothesized that, from the ants' viewpoint, the lipid-rich fruits may be chemically analogous to their insect prey, an idea supported by the comparison made by Hughes et al. (1994) between the fatty acid composition of elaiosomes, lipid-rich food bodies of typical myrmecochorous fruits, and insects. Given that elaiosomes and the arils of lipid-rich fruits are chemically and morphologically similar structures (Hughes et al. 1993), it is possible that harvestmen use these fruits more often than we have previously suspected.

We are grateful to P.S. Oliveira, A.V.L. Freitas and two anonymous reviewers for helpful comments on the manuscript; to the Fundação Florestal do Estado de São Paulo for permitting our work at Parque Intervales. The study was supported by fellowships from FAPESP to M.A. Pizo, and CAPES to G. Machado.

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SHORT COMMUNICATION

HOMALONYCHUS THEOLOGUS (ARANEAE, HOMALONYCHIDAE): DESCRIPTION OF EGGSACS AND A POSSIBLE DEFENSIVE POSTURE

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ABSTRACT. Presented here is a description of the cryptic, sand-covered eggsacs of *Homalonychus theologus*. Additionally, when this species is gently harassed, it adopts a rigid, paired-leg position which may be a defensive posture functioning in immobility and possibly mimicking cactus spines.

Keywords: Spider, eggsac, defensive behavior, immobility

The spider family Homalonychidae is represented by a single North American genus consisting of two species. *Homalonychus* spiders are found in the deserts of extreme southeastern California, the southern tip of Nevada, southwestern Arizona, northwestern Sonora, and Baja California. These spiders are not commonly encountered, and the sparse information that is known regarding its natural history was presented by Roth (1984). We had the opportunity to examine a few individuals of *H. theologus* Chamberlin 1924 and present our observations on two aspects.

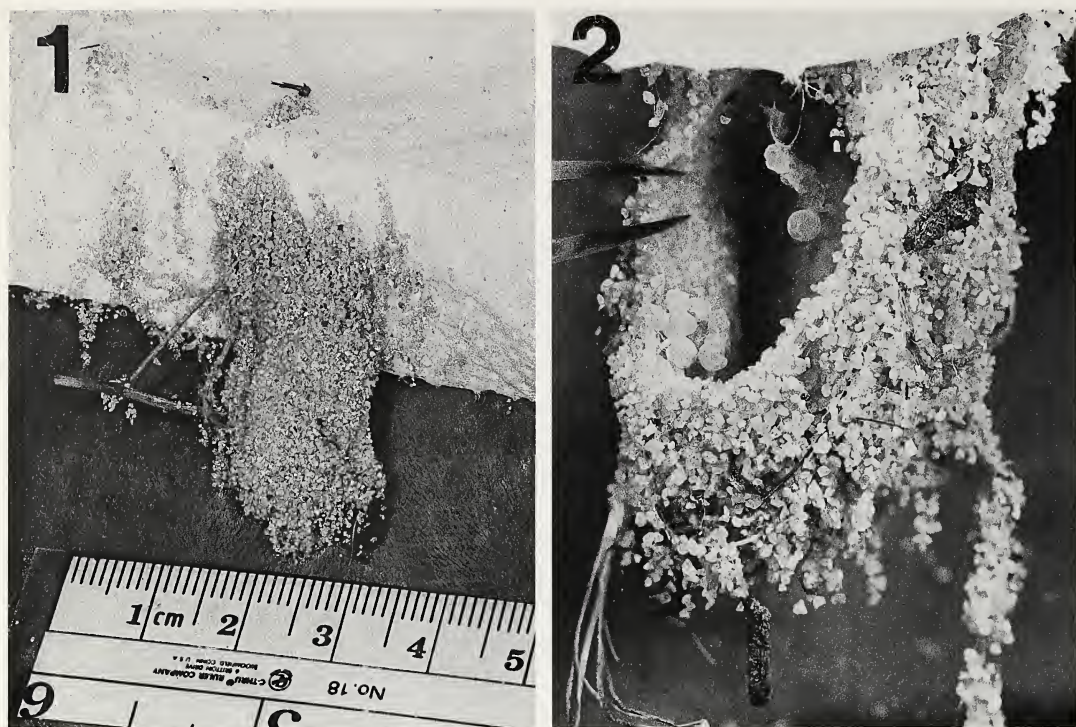
Eggsacs.—Roth (1984) mentioned only one eggsac for the genus that was collected in April but “nothing is recorded regarding either the placement of the egg sac or its description.” In the original description of *H. positivus* (= *H. selenopoides* Marx 1891), Chamberlin (1924) reported a collection from Guaymas, Sonora, Mexico, in which three females were “taken under stones with egg sacks” on 12 April 1921. Because the specimens reported by Chamberlin were type specimens which Roth might have studied for his revision, it is possible that the eggsac mentioned by Roth was from the same collection. Apparently, Roth overlooked the information presented by Chamberlin.

Two female *H. theologus* were captured (California: San Bernardino County, ♀ #1, off Amboy Rd by Sheep Hole Pass, 640 m, 16 February 1997, M. Holman, O. Trout; ♀ #2, 5 km S Amboy, 150 m, on salt flat under a board, 25 April 1998, R. Vetter) and maintained in 2.5 liter plastic containers with sand substrate. (♀ #1 had beach sand and ♀

#2 had sand from its natural habitat.) Crumpled paper toweling served as refugia, and females were maintained until death. Upon cleaning out their containers within two days of each female’s death, it was discovered that in the hidden recesses of the paper towels, each spider had produced two rounded, sand-covered eggsacs (Fig. 1). The eggsacs were about 18 mm in diameter and smooth inside, being lined with silk (Fig. 2).

Eggsacs from ♀ #1 were transferred to a 4 liter plastic jar and maintained in the first author’s home at temperatures of 24–30 °C. Spiderlings were first noticed on the toweling 53 days later although the development time probably was longer because the date of oviposition was unknown. Seventeen spiderlings were collected, and examination of the eggsacs revealed 22 shed skins in one eggsac and no evidence of shed skins, spiderlings nor infertile eggs in the other. Eggsacs of ♀ #2 were removed from the female’s container and examined. One contained 17 shed skins and 8 desiccated, presumably infertile eggs; it is unknown where the spiderlings dispersed. The other eggsac contained 20 spiderlings and one desiccated egg. Sixteen of the 20 spiderlings appeared to have died molting from the 1st to 2nd instar; of the remaining four, two were dead and two were moribund. No spiderlings were found outside of the eggsacs.

Although the maintenance of these spiders was artificial, the eggsacs were similar in construction to one observed under a rock in Punta Diggs (17 km S San Felipe, Baja California Norte, Mexico, under rocks on sandy desert soil, S. Johnson, pers.



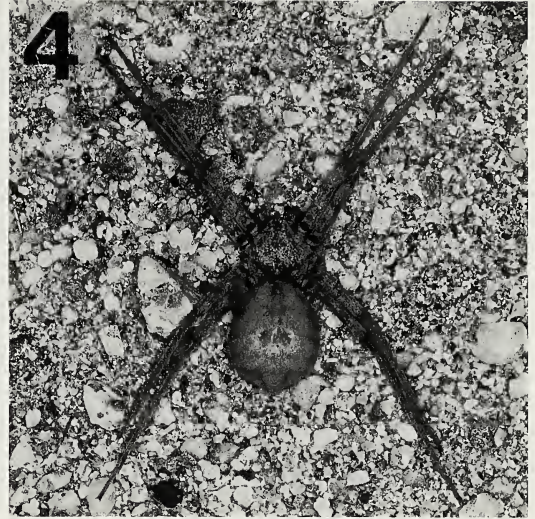
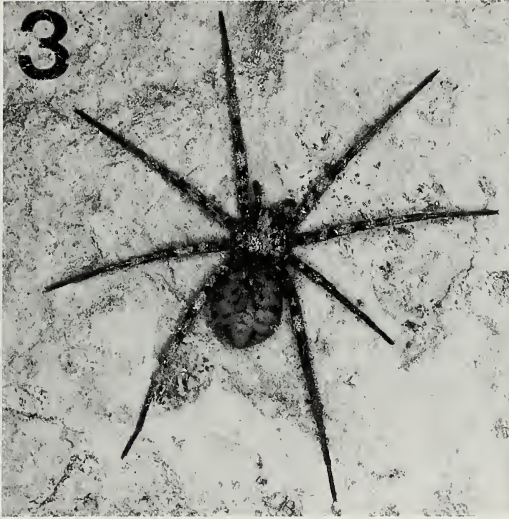
Figures 1, 2.—Eggsacs of *Homalonychus theologus*. 1. Sand-covered eggsac of *Homalonychus theologus* suspended from the underside of a paper towel; 2. Close-up of eggsac with view of inside. An egg is visible in the interior of the sac. (Photos by P. Kirk Visscher)

comm.). In our artificial setting, *H. theologus* produced 21, 22, and 25 eggs per eggsac. These females were probably fed only about once per month and, therefore, the egg total here may be low due to the sparse food supply. Because we collected one specimen at night while it roamed around in sparsely vegetated desert yet saw none during the day while conducting experiments over extensive periods of time in the same locale, we speculate that *H. theologus* spiders spend daytime in rodent burrows and under rocks where they easily could affix their eggsacs. The sand and silk covering would probably aid in humidity/temperature control as well as camouflaging the eggsac to avoid detection by potential predators or parasites. Although *Homalonychus* spiders are found partially buried in sand (Roth 1984; pers. obs.), they do not appear to construct burrows nor remain hidden in the sand during the daylight hours.

Potential defensive posture.—When at rest, *Homalonychus* spiders position themselves with all legs spread out from one another (Fig. 3; also see Roth 1984: fig. 14). When disturbed, *H. theologus* shifts its legs to a rigid “paired-leg” formation (first two legs forward, hind two legs rearward) (Fig. 4). When a mature (12 mm body length) female (California: *Riverside County*, Cactus City, 17 km W Chiriaco Summit off I-10, 400 m, at night wander-

ing, 23 March 1997, R. Vetter) was held by her legs with a pair of forceps she could be rotated in all positions without becoming limp or attempting to run. This behavior can also be elicited by touching the spider with a pencil or forceps, when at rest or while moving, day or night. However, a 3 mm *Homalonychus* juvenile from the same locale did not adopt this posture when chased for several minutes in two separate trials. Therefore, propensity to display this behavior may be size dependent (i.e., the spider's potential as a prey item). When a penultimate *H. theologus* female (9 mm body length) was uncovered under a rubber tire, (California: *San Bernardino County*, 5 km S Amboy, 150 m, 26 April 1998, R. Vetter), she moved several cm from her initial spot, became immobile, adopted the “paired leg” stance (which was maintained while being maneuvered into a 40 dram vial, slid down the length of the vial and did not abandon this position until she was slid back out of the vial into the collector's hand).

We did not have sufficient numbers of specimens to attempt additional tests and, therefore, we can only speculate on the mechanism of the behavior if, indeed, it is defensive in function. The primary defenses of *H. theologus* are nocturnal activity and crypsis including burial in sand, the cryptic aspect of which is enhanced by the spider's dorsal hairs



Figures 3, 4.—Postures of *Homalonychus theologus*. 3. Characteristic resting posture of *Homalonychus* with legs held flat and spread equidistant from one another. This penultimate male molted and was not placed back on sand. Hence, it shows its natural coloration without sand trapped amongst hairs; 4. Posture of a female *H. theologus* with rigid body and paired legs, possibly a defense mechanism. (Photos by J. C. Cokendolpher)

which trap small sand grains (except in mature males) (Roth 1984). Immobility is a common general defense among animals (Cott 1940). Cloudsley-Thompson (1995) mentions death-feigning (thanatosis) in an exhaustive review of spider defensive behaviors; however, no behavior such as we have seen in *H. theologus* is mentioned. Additionally, thanatosis in spiders usually involves holding the legs tucked in close to the body. The rearrangement of the legs in *H. theologus* is somewhat puzzling as two legs held together would seem to increase the spider's conspicuousness, and hence belie its cryptic nature. Possibly, this leg orientation provides a novel image to a predator accustomed to eating spiders. Predators are known to avoid novel stimuli (Cott 1940) although we doubt that predators will care whether its prey have "4" or 8 legs. We would like to offer one additional speculative hypothesis. Because *H. theologus* is both nocturnal and a desert dweller, possibly the immobility in concert with paired-leg posture mimics the appearance of detached spines of dead cactus which could be an effective defense in the desert at night when visibility is poor.

Voucher specimens are housed at the California Academy of Sciences.

We thank M. Holman and O. Trout for providing us the first ovipositing female and S. Johnson for sharing information on his observations of an egg-sac in Mexico.

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ARACHNOLOGICAL RESEARCH FUND

The AAS Fund for Arachnological Research (AAS Fund) is funded and administered by the American Arachnological Society. The purpose of the fund is to provide research support for work relating to any aspect of the behavior, ecology, physiology, evolution, and systematics of any of the arachnid groups. Awards may be used for field work, museum research (including travel), expendable supplies, identification of specimens, and/or preparation of figures and drawings for publication. Monies from the fund are not designed to augment or replace salary.

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Citation of references in the text: Cite only papers already published or in press. Include within parentheses the surname of the author followed by the date of publication. A comma separates multiple citations by the same author(s) and a semicolon separates citations by different authors, e.g., (Smith 1970), (Jones 1988; Smith 1993), (Smith 1986, 1987; Smith & Jones 1989; Jones et al. 1990). Include a letter of permission from any person who is cited as providing unpublished data in the form of a personal communication.

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Lombardi, S.J. & D.L. Kaplan. 1990. The amino acid composition of major ampullate gland silk (dragline) of *Nephila clavipes* (Araneae, Tetragnathidae). *Journal of Arachnology* 18:297–306.

Krafft, B. 1982. The significance and complexity of communication in spiders. Pp. 15–66, *In* Spider Communications: Mechanisms and Ecological Significance. (P.N. Witt & J.S. Rovner, eds.). Princeton University Press, Princeton, New Jersey.

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first journal page to indicate current address or other information concerning the author. These are placed together on a separate manuscript page. Tables and figures may not have footnotes.

Running head.—The author's surname(s) and an abbreviated title should be typed all in capital letters and must not exceed 60 characters and spaces. The running head should be placed near the top of the title page.

Taxonomic articles.—Consult a recent taxonomic article in the *Journal of Arachnology* for style, or contact the Subject Editor for Systematics. Papers containing the original taxonomic description of the focal arachnid taxon should be listed in the Literature Cited section.

Tables.—Each table, with the legend above, should be placed on a separate manuscript page. Only horizontal lines (usually three) should be included. Tables may not have footnotes; instead, include all information in the legend. Make notations in the text margins to indicate the preferred location of tables in the printed text.

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Legends for illustrations should be placed together on the same page(s) and separate from the illustrations. Each plate must have only one legend, as indicated below:

Figures 1–4.—*A-us x-us*, male from Timbuktu: 1. Left leg; 2. Right chelicera; 3. Dorsal aspect of genitalia; 4. Ventral aspect of abdomen.

Figures 27–34.—Right chelicerae of species of *A-us* from Timbuktu: 27, 29, 31, 33. Dorsal views; 28, 30, 32, 34. Prolateral views of moveable finger; 27, 28. *A-us x-us* holotype male; 33, 34. *A-us y-us* male. Scale = 1.0 mm.

Assemble manuscript for mailing.—Assemble the separate sections or pages in the following sequence; title page, abstract, text, footnotes, tables with legends, figure legends, figures.

Page charges and reprints.—There are no page charges, but the author will be charged for changes made in the proof pages. Reprints are available only from the Allen Press and should be ordered when the author receives the proof pages. Allen Press will not accept reprint orders after the paper is published.

SHORT COMMUNICATIONS

The above instructions pertaining to Feature Articles apply also to Short Communications, which should be prepared in the same manner as regular Feature Articles. Short Communications are usually limited in length to three journal pages, including tables and figures. They will be printed in a smaller (10 point) typeface.

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